

BULLETIN
of **CARNEGIE MUSEUM OF NATURAL HISTORY**

**APPENDICULAR MYOLOGY AND RELATIONSHIPS OF
THE NEW WORLD NINE-PRIMARYED OSCINES
(AVES: PASSERIFORMES)**

ROBERT J. RAIKOW

*Research Associate, Section of Birds,
Carnegie Museum of Natural History, and
Department of Biological Sciences,
University of Pittsburgh, Pittsburgh, Pennsylvania 15260*

BULLETIN OF CARNEGIE MUSEUM OF NATURAL HISTORY

Number 7, pages 1-43, figures 1-10, tables 1-5

Issued 17 November 1978

Price: \$3.50 a copy

Craig C. Black, *Director*

Editorial Staff: Hugh H. Genoways, *Editor*; Duane A. Schlitter, *Associate Editor*;
Stephen L. Williams, *Associate Editor*; Teresa M. Bona, *Technical Assistant*.

© 1978 by the Trustees of Carnegie Institute, all rights reserved.

CARNEGIE MUSEUM OF NATURAL HISTORY, 4400 FORBES AVENUE
PITTSBURGH, PENNSYLVANIA 15213

CONTENTS

Abstract	5
Introduction	5
Problems of Phylogeny Construction	5
Monophyly of the New World Nine-primaried Oscines	7
Materials and Methods	10
Dissection	10
Nomenclature	10
Determination of Primitive and Derived States	10
Muscles of the Forelimb	11
Muscles of the Hindlimb	17
Characterization of Taxa	25
Vireonidae	25
Parulidae	26
Thraupidae	28
Coerebidae	31
Emberizinae	31
Cardinalinae	31
Icteridae	32
Carduelinae	32
Drepanididae	33
A Phylogeny of the New World Nine-primaried Oscines	34
Cluster 1	35
Cluster 2	35
Cluster 3	38
Cluster 4	39
Cluster 5	39
Cluster 6	39
Proposed Classification	40
Conclusions	41
Acknowledgments	42
Literature Cited	42

ABSTRACT

The gross morphology of the forelimb and hindlimb muscles was studied in approximately 100 species of songbirds, and analyzed cladistically to construct a phylogeny of the New World nine-primaried oscines. Methods and problems of phylogenetic analysis are discussed, and the rationale for the proposed phylogeny is presented. It is suggested that the Parulidae are the

most primitive family of the group, the Thraupidae somewhat more advanced, and the Fringillidae and their descendants the most highly derived. The Icteridae may be the sister group of the Emberizinae, with *Spiza* as a link. The Drepanididae arose from the Carduelinae. The position of various problematic genera is discussed.

INTRODUCTION

This is a study of the evolutionary relationships in a large assemblage of songbirds, the New World nine-primaried oscines. The relationships among passerine birds continue to be unclear despite many studies attempting to unravel the pattern of their affinities. This is because of the large number of species, genera, and families involved, the general lack of distinctive characters defining specific groups, the tendency of groups to intergrade, and the high frequency of parallel and convergent similarities, especially in the suborder Oscines (Passeres). These problems are apparent in the confused taxonomic situation. On the one hand there has been a tendency to combine great numbers of species into large and unwieldy families, as in the treatment of the broadly defined Muscicapidae and Emberizidae of the Check-list of Birds of the World. On the other hand many small (often monotypic) families have been created for forms whose relationships to larger groups are undetermined, such as the Tersinidae, Catamblyrhynchidae, and Zeledoniidae. The family names used herein are those of Wetmore (1960) unless otherwise stated. If any sense is to be made of the oscine problem, the first task will have to be to cluster the large families into groups of apparently related forms, and then to analyze these groups individually. Affinity in this case should be based on evolutionary rather than purely phenetic relationships, that is, superfamilial assemblages should be hypothesized to be monophyletic. If the hypothesis of monophyly withstands scrutiny, the next step should be to analyze evolutionary relationships *within* each assemblage, that is, to develop a phylogeny of the families involved. In the course of this process an attempt should be made to determine to which large family each small family has its closest relationships, so that they may be combined where possible, and the number of families reduced. Once the phylogeny of several such assemblages has been determined, then the phylo-

genetic relationships between them may be analyzed, and gradually an overall phylogeny of the suborder Oscines can be constructed. Any attempt to work out relationships within the whole suborder by individual family comparisons is probably doomed to failure because of the complexity of the situation and the number of families involved.

This paper reports the results of an attempt to analyze the relationships within one large suprafamilial assemblage of the suborder Oscines. The New World nine-primaried oscines have traditionally been regarded as some sort of "natural" group, although various authors have differed on which families should be included, as well as on the rank to be given various groups. For the purpose of analysis I have included all of the groups that various authors have considered part of the assemblage. These are the Vireonidae (including the Vireolanidae and Cyclarhidae), Parulidae, Zeledoniidae, Thraupidae, Coerebidae, Tersinidae, Catamblyrhynchidae, Fringillidae (including the Emberizinae, Cardinalinae, and Carduelinae), Icteridae, and Drepanididae. Together these comprise a significant number of species, approximately 955, which amounts to roughly 11% of living species of birds, 19% of living species of passeriformes, and 24% of living species of oscines.

PROBLEMS OF PHYLOGENY CONSTRUCTION

In any analysis of the evolutionary history of a group of organisms, several problems must be overcome, and the first is to choose a method of analysis. Assuming that evolution really has occurred, there must be a true phylogeny of the taxa under study, but we have no sure way to know what this is, or whether we have found it. In practice, then, a phylogeny is a hypothesis that may be presented for subsequent corroboration or refutation. Any method of analysis may be used to hypothesize a phylogeny. Many workers have constructed

branching diagrams (dendrograms) that they hypothesize to be phylogenies on the basis of shared similarities. In current terminology this would be termed a phenetic method, whether done by traditional methods of clustering taxa by resemblance, or by modern computer techniques. A more rigorous approach is advocated by followers of the cladistic school, who construct dendrograms by clustering "sister groups" on the basis of shared derived character states (synapomorphies) only. The differences between the phenetic and cladistic philosophies have engendered much vigorous and often rancorous discussion, though one has the impression that the philosophical differences are greater than the results that the two methods produce. It appears to me that both approaches represent extremes to which practical students need not limit themselves, and I expect that some intermediate position, containing contributions from both camps, will probably become the standard approach in the coming years. In the present study I will use mainly the cladistic method of analysis, but where this falters I will not hesitate to employ more traditional approaches. I see no justification for ignoring information that cannot be forced into a cladistic mold. While one good synapomorphy may be better than many "similarities," several solid similarities are still probably better in suggesting relationships than a trivial or contrived synapomorphy.

Once cladistics has been chosen as the principal method of phylogeny construction, several other problems arise: (1) It must be established that the taxon under analysis is monophyletic; (2) A sufficient number of characters must be found whose primitive/derived polarity can be determined with confidence; (3) Character conflicts must be resolved; (4) A consistent philosophy of evolutionary probabilities must be maintained. These points will be discussed individually.

(1) One could probably do a cladistic analysis of any collection of taxa, but unless the group can be shown to be probably monophyletic, there is little reason to suppose that the result represents a true phylogeny. To demonstrate monophyly, the most convincing arguments are demonstrations that the taxa comprising the group share one or more synapomorphies. If this is done, the existence of phenetic similarities will strengthen the hypothesis of monophyly. A hypothesis based on such similarities alone, however, is less convincing.

My analysis is based mainly on new information from the limb muscles, but first I will review other

kinds of information to establish the likelihood that the New World nine-primaried assemblage is indeed monophyletic. Nevertheless, at the outset the hypothesis of monophyly should be presented as such, and after the analysis of new data is completed, this hypothesis should be reexamined to see whether the new information supports or refutes it. If it is supported, then the hypothesis of monophyly is strengthened, the proposed phylogeny may be taken as reasonable, and the whole exercise is justified. If it is refuted, then the major result of the study may be to show that a group formerly considered monophyletic or "natural" is not so, leading to the necessity for a reevaluation of its relationships.

(2) One of the greatest problems in cladistic analysis is finding a sufficient number of characters that can be analyzed to determine primitive to derived polarities. The more characters available, the greater the number of branching points that can be placed in a proposed phylogeny. Also, the validity of branching points is increased if more than one character shift can be indicated at each, especially if they are not parts of a single adaptive complex. The lower the categorical level of the group being analyzed, the more difficult it is to find many characters useful in analysis. The New World nine-primaried oscines are a particularly difficult group in this respect because they differ little in major features, while at the same time having undergone an enormous amount of speciation.

(3) Character conflicts arise when different characters indicate different branching patterns. Some characters must, therefore, have arisen independently in different lineages by convergence, parallelism, or evolutionary reversals, giving rise to false synapomorphies. This is especially troublesome in the lower taxonomic categories with groups that share a similar genetic background, and when the character states themselves are of a relatively simple nature, such as losses of structures or minor structural modifications. Although we may realize that these conflicts can result from recognized biological processes, in many specific cases it will be difficult or impossible to determine which alternative branching pattern is most likely to reflect the actual evolutionary history of the group. In such cases the expedient solution is to adopt the simplest pattern, or to attempt to correlate different characters so as to arrive at a reasonable solution. I emphasize strongly that it is impractical to expect that any phylogeny will be without some character

conflicts, but if it is recognized that these situations arise through ordinary biological processes, one need not refrain from developing a phylogenetic hypothesis that reflects the best fit available with the data at hand.

(4) In phylogenetic analysis, as in any branch of science, there may be a tendency to lose sight of the overall problem when confronted with a mass of individual data. In cladistics the problem is to maintain an overview of the whole evolutionary picture while dealing with many individual character phylogenies. In analyzing the New World nine-primaried oscines I will adhere to a model of evolution that postulates (a) that new major adaptations arise by the gradual modification of preexisting states, and (b) that the development of a new major adaptive feature may be followed by extensive radiation into specialized subdivisions of the new adaptive zone. Thus, in developing a phylogeny of these birds, I will hypothesize that the major family and subfamily groups represent secondary radiations in new adaptive zones associated primarily with feeding specializations. This hypothesis will be tested by comparing the correlation between feeding adaptations and modifications of the locomotor apparatus.

MONOPHYLY OF THE NEW WORLD NINE-PRIMARIED OSCINES

This group is generally but uncritically regarded as monophyletic, an idea based mainly on several lines of evidence that I will review below. Some of this evidence can be interpreted in terms of primitive and derived character states, even though it may previously have been presented in more traditional phenetic terms, and such evidences give the most convincing arguments in favor of monophyly. Other evidences cannot be interpreted in this way, and must be considered only in terms of general similarity. I do not agree with those who believe that such data are of no use in phylogenetic analysis. Such information may not be helpful in determining the exact pattern of branching points in a phylogeny, but it does indicate genetic similarity between taxa and can at least be used to support hypotheses about clusters of related forms within a larger group. The purpose of this section is not to analyze relationships *within* the New World nine-primaried complex, but to examine the likelihood that the group as a whole is monophyletic, which is a necessary precondition for a cladistic analysis of its subgroups. This hypothesis of monophyly will

be reexamined after the limb muscle data have been analyzed to see whether the new information will corroborate or refute the idea of monophyly. It will be seen that neither earlier studies nor the present investigation support the inclusion of the Vireonidae in the New World nine-primaried oscine assemblage. Nevertheless, they are included here because they have traditionally been grouped with this assemblage.

Number of primaries.—The number of primary feathers varies among birds, but is usually constant within a family. The number may be reduced (or occasionally increased) among flightless forms, but in flying birds it varies from 10 to 12. In passeriformes the number is 10, but the tenth (outermost) primary is sometimes reduced to a vestige, and such birds are referred to as nine-primaried (Van Tyne and Berger, 1976:127–129). In all, this suggests that the nine-primaried condition among passerines is a derived state, and that a "functional" tenth primary is primitive.

Most of the New World nine-primaried oscines have only a vestigial tenth primary, except for some of the vireonids (*Cyclarhis*, *Vireolaninus*, and some vireos, Mayr and Amadon, 1951:27). There are several other nine-primaried oscine families as well, such as the Zosteropidae, Hirundinidae, Alaudidae, and Motacillidae. These families do not appear to be closely related to the New World nine-primaried oscines, however, and most probably acquired a reduced tenth primary independently of them. Thus, except for the vireonids, the New World nine-primaried oscine assemblage is linked by this condition, which may be reasonably interpreted as a synapomorphy supporting the hypothesis that the group is monophyletic.

Pneumatic fossa.—A well-developed second pneumatic fossa of the humerus is a derived condition, whereas the primitive state is the presence of only one fossa (Bock, 1962:437). The derived state occurs in several oscine families, some of which are not closely related, suggesting parallel evolution of this state. Bock (1962:432) pointed out that the New World nine-primaried oscines ". . . appear to be the only larger subgroup within the oscines, that is rather uniform in having a fully developed condition." Again, the Vireonidae are an exception, having ". . . only the beginnings of the second fossa" (Bock, 1962:432). A few genera of Icteridae also have only a small second fossa, but because their familial position is unquestioned, this is best interpreted as a case of secondary reduction.

Tongue apparatus.—In a study of the skeleton and certain muscles of the tongue of songbirds, George (1962, 1968) found two correlated differences between the New World nine-primaried oscines and other families. The basihyale, an unpaired bone forming part of the central axis of the tongue skeleton, is laterally flattened in the Coerebidae, Drepanididae, Parulidae (except *Peucedramus*), Icteridae, Catamblyrhynchidae, Thraupidae, and in the cardueline, cardinaline, and emberizine finches. In 20 other oscine families, including the vireonids, cyclarhids, vireolaniids, and Tersinidae, it is cylindrical rather than flattened in cross section. There is a related variation in the hyoglossus obliquus muscle (which George termed the hypoglossus posterior). This muscle arises from the posterior processes of the paraglossalia, passing transversely beneath the basihyale without inserting on it (condition A) in most families examined. However, it is partly or completely attached to the basihyale (condition B) in the New World nine-primaried oscines except for the Cyclarhidae, Vireonidae, and *Peucedramus* (not determined for *Vireolanus* or *Tersina*). The cylindrical basihyale always occurs together with the unattached muscle (condition A) except in swallows (cylindrical and B), whereas in the Certhiidae a compressed basihyale also occurs with condition B. Because neither swallows nor creepers are closely related to the New World nine-primaried oscines, these exceptions need not concern us. The correlation of the compressed basihyale with the attached hyoglossus obliquus suggests a functional relationship, so these two characters will be regarded as a single complex character. The fact that the New World nine-primaried assemblage as a whole stands apart from many other oscine families in this character argues, at least on phenetic grounds, that they form a related group.

This suggestion would be greatly strengthened if it could be shown that the tongue condition in the New World nine-primaried oscines is a derived state. George (1962, Table 1) recognized two character states for the hyoglossus obliquus as already noted—A (not inserted on the basihyale), and B (inserted on the basihyale). This is a simplification, however, as there are variations in condition B. George recorded three variations, as shown in his figs. 5B–D and 6B–D. One is a condition peculiar to the Hirundinidae, which need not concern us. The condition shown in Figs. 5C and 6C has some fibers inserting on the basihyale, while a deeper layer passes beneath the bone. The condition shown

in Figs. 5D and 6D has all fibers inserting on the basihyale, with none passing beneath it. There is some confusion in interpreting George's explanation because in his Table 1 he lists only the conditions A and B noted above, whereas in the text he notes conditions A (as in Table 1), B (as in the Hirundinidae, corresponding to Figs. 5B and 6B), and C (corresponding to Figs. 5C, D and 6C, D). Thus several variants are combined under condition B of Table 1, and it is not apparent which variant occurs in any given species having this general condition B.

These variations may be interpreted as stages in a morphocline. Either the hyoglossus obliquus is primitively attached to the basihyale, and is progressively losing this connection in some forms, or alternatively it is primitively not attached and is progressing to an inserted state. Which is the most likely direction of evolutionary change?

I believe that the condition in the New World nine-primaried oscines, with the hyoglossus obliquus attached to a flattened basihyale, is the derived state for the following reasons: (1) The cylindrical basihyale with no muscle insertion occurs in Alaudidae, Corvidae, Paridae, Sittidae, Chamaeidae, Cinclidae, Troglodytidae, Mimidae, Turdidae, Sylviidae, Motacillidae, Dulidae, Bombycillidae, Ptilogonatidae, Laniidae, Cyclarhidae, and Vireolaniidae (George, 1962, Table 1). These groups represent a great variety of different adaptive types with many different feeding specializations. It would seem most likely that the occurrence of the same structural conditions in all these different groups would be due to inheritance from a common ancestor, with the different condition in the New World nine-primaried oscines being related to some specialization in early members of this group. George (1962) argues that it is a specialization for more firmly attaching the movable tongue to the hyoid skeleton. (2) George (1962:27) notes that in the development of "*Setophaga picta*" (= *Myioborus pictus*) (Parulidae) from the nestling to the fledgling stage, the developing basihyale becomes progressively more flattened. Possibly this ontogenetic change parallels a phylogenetic change in the shape of the bone from a primitive to a derived state. As with any criteria for determining morphocline polarity, these are not without uncertainty, but on the whole it appears more likely than not that the condition of the tongue apparatus in the New World nine-primaried oscines is derived relative to the condition in oscines generally.

Egg-white proteins.—Sibley (1970) studied rela-

tionships among passerine birds by electrophoresis of egg-white proteins. The New World nine-primaried oscines were found to have similar electrophoretic patterns, even to the point where some groups generally recognized as families were virtually indistinguishable. Data of this sort cannot be analyzed cladistically because the direction of evolutionary change of the protein molecules is not known; indeed differences in molecular structure are only indirectly estimated by the procedure. This is because the technique does not examine molecular structure directly, but only electrophoretic mobility, which has a close but imperfect correlation with molecular structure as coded in the genes. Therefore, as Sibley (1970:21) makes clear, what is measured is "genetic relatedness," not genealogy. Nevertheless, this information is useful in the present context since I am concerned not only with cladistic genealogy, but also with the nature and amount of evolutionary change in evolving lineages between branching points. The close similarity in proteins indicates a close similarity in the genes coding for their production, and by any philosophy this is a strong indication that the various members of the New World nine-primaried oscine assemblage share a common genetic background. This strongly supports the idea of monophyly of the assemblage, even though it does not contribute to an analysis of its phylogenetic branching pattern.

Distribution and adaptive diversity.—The New World nine-primaried oscines occur mainly in the New World as their name implies; the exceptions are probably offshoots from this center of distribution and presumed origin. The coherence of the group suggests that the various families are inter-related as parts of a single adaptive radiation in the New World, and that the family groups correspond roughly to major adaptive niches based mainly on feeding specializations. Thus the Parulidae are mainly insectivorous; the Thraupidae, rather omnivorous but with a strong reliance on fruits; the Emberizinae may be characterized as mainly terrestrial foragers on relatively small seeds; the Carduelinae are mainly arboreal feeders on larger seeds; the Icteridae are marked by a specialized biomechanical system involving forceful jaw gaping into crevices, for opening fruits, and so forth. The Drepanididae are a special case; founded by a cardueline ancestor (Raikow, 1977b), the family radiated into an unusually wide variety of feeding niches in the absence of ecological competitors.

Sibley (1970:107) warns against overreliance on

feeding specializations; the possibility of convergence provides a danger of classifying feeding niches rather than organisms. Nevertheless, there is also a possibility that useful taxonomic characters may be needlessly shunned by the fear that if adaptive, they are subject to convergence. Some organisms must be similar because of ancestry rather than convergence, and I think it probable that the major families of New World nine-primaried oscines represent the products of secondary radiations, arising when an ancestor entered a new adaptive zone. In the present case this idea is generally supported by the anatomy of the limb muscles as discussed below; this is important because these muscles are not part of the adaptive complex of the feeding mechanism.

These New World families often appear to be ecological equivalents of unrelated Old World families that have independently radiated into similar broadly-defined adaptive niches. Thus, for example, the Parulidae correspond to the Sylviidae, and the "New World finches" (Emberizinae and Cardinalinae) to the Ploceidae and Estrildidae. The Carduelinae, however, are widely distributed and ecologically diverse in both areas, and especially in the Old World. The Icteridae correspond to the Sturnidae.

In general, then, the cohesive assemblage of New World nine-primaried oscines presents a picture of distribution and specialization that is most reasonably interpreted as resulting from an evolutionary radiation into various broad feeding niches, with secondary radiations within each adaptive zone, and paralleling a separate pattern of similar radiations among other taxa in the Old World. This picture supports the idea that the group is monophyletic.

Pterylosis.—The unity of the nine-primaried New World oscine group is also attested to by the pterylosis. According to Mary H. Clench (personal communication) "aside from the distinctive pattern found in vireos (including *Cyclarhis* and *Vireolanus*) the body pterylosis of the New World nine-primaried oscines is relatively uniform. Minor differences in tract geometry and numbers of feathers may serve to group some genera, or to indicate certain family divisions, but the overall similarity of the pterylosis of this assemblage is striking."

Indistinct boundaries.—Although the New World nine-primaried oscines are usually classified in several separate families, the boundaries between them are often indistinct and arbitrary, many genera

being intermediate between the typical members of different families. This indicates that the group is cohesive and closely interrelated. Indeed, some authors have suggested merging them into a small number of families in the light of these difficulties. For example Sibley (1970) reduced the assemblage (excluding the vireonids) to a single family Fringillidae, with three subfamilies and nine tribes.

In the preceding discussion the hypothesis that the New World nine-primaried oscine assemblage (possibly excluding the Vireonidae) is monophyletic has been supported by various lines of evidence. Some of these, including the number of primaries,

the pneumatic fossa of the humerus, and the tongue apparatus, appear to be derived character states grouping these taxa apart from other oscines. Other evidences, including the indistinct boundaries between families, the egg-white proteins, the pterylosis, and the geographic distribution and pattern of adaptive diversity, are not readily interpretable in cladistic terms, but nevertheless offer supporting evidence in favor of the theory of monophyly. Individually, each type of evidence generates a certain degree of confidence in the hypothesis; taken together they reinforce each other to further strengthen the hypothesis.

MATERIALS AND METHODS

DISSECTION

The forelimb and hindlimb muscles were dissected in nearly 100 species of songbirds (listed in Tables 2 and 3). Dissection was carried out under a stereomicroscope at magnifications of 6× to 25×, and the muscles were stained with iodine (Bock and Shear, 1972) to render fiber arrangement more visible. Detailed descriptions of the muscles were prepared for a reference species, *Loxops virens*, and are presented elsewhere (Raikow, 1976, 1977a). In the present study the muscles in each species are compared to those of *L. virens* and only the differences are noted. Drawings were made with a camera lucida attachment to the microscope.

Berger (1969) reviewed the variations in passerine appendicular muscles. He listed various muscles for which knowledge of structure and variation is uncertain or ambiguous. In the following account further information will be provided to clarify these problems with regard to the groups studied herein.

NOMENCLATURE

The nomenclature of avian myology has a long and confusing history. Many workers have applied different names to the same muscle and the same name to different muscles. Some have occasionally attempted to stabilize the nomenclature for groups of muscles, but with only partial success. Most recently Berger (George and Berger, 1966) presented a standardized nomenclature for the entire avian muscular system. In the present study I have made some changes from that system to conform with a new system of names being developed by the International Committee of Avian Anatomical Nomenclature for publication as the *Nomina Anatomica Avium* (N.A.A.), which is intended to stabilize avian anatomical nomenclature in all branches of avian biology. The names for muscles used herein are those tentatively adopted for the N.A.A. at the time this is written. Synonyms with the nomenclature of Berger are given in my previous papers (Raikow, 1976, 1977a).

DETERMINATION OF PRIMITIVE AND DERIVED STATES

There are no certain methods for determining the direction or polarity of evolutionary change in an evolving character, but

several criteria have become generally accepted as being reasonably reliable. The most common is out-group comparison. If a character varies within a group, and one of the variants also occurs in a related outside group, then the character state that occurs in both groups is considered primitive within the group being studied. Another method is in-group comparison. Within the group under study, the primitive state is considered likely to be that which is distributed among a variety of different subgroups. Ross (1974) and Kluge (1977) discuss the rationales underlying these and other methods of determination. Out-group comparisons are the principal method used in this study to determine character states, while in-group comparisons are used occasionally. I have tried to explain in the text the basis for each individual determination so that its validity may be examined. This practice is not always followed by students of cladistics.

For doing out-group comparisons it is important to choose taxa that are appropriate for comparison to the in-group. The general opinion is that proper out-groups should be of about the same categorical level as the in-group, and closely related to it so as to minimize the chances of convergence. Ideally an out-group should be the sister group of the in-group, but in practice this may be impossible to carry out because the sister group is not known. The practical approach is to choose groups that appear to be closely related to the in-group even though their precise cladistic relationships are unknown. In this study I have chosen certain likely out-groups for examination and have considered in addition the literature on more distant relatives. Thus, the muscle variations in birds generally are first examined, with particular emphasis on passerines (information summarized by George and Berger, 1966). To this I have added new observations on limb muscles from unpublished studies now underway in my laboratory. Clench and Austin (1974) summarized the ideas of various workers on the relationships of passerines as expressed in linear arrangements, and this has aided me in choosing groups for comparison. In their own arrangement the Nectariniidae, Estrildidae, and Ploceidae are grouped with the New World nine-primaried oscines, along with a few other families, so I have included a nectariniid in my dissections, and also have used the extensive observations of Bentz (1976) on the Ploceidae and Estrildidae. No principally New World oscine family appears close to the New World nine-primaried oscines, and in the Old World, many families are either highly specialized

(for example, Paradisaecidae, Hirundinidae) or are small or of limited distribution (for example, Artamidae, Irenidae) and, therefore, seem to be unlikely candidates for a sister-group relationship with the New World nine-primaried oscines. I have, therefore, concentrated my dissections on a small group of relatively unspecialized, mainly insectivorous, and evolutionarily successful Old World forms in the Sylviidae. These appear, rather intuitively, to lie near the origin of the New World nine-primaried oscines. My dissections of the limb muscles of these groups, and the work of Bentz (1976) on the ploceid-estrilidid

complex confirm that these groups are close to the New World types because their limb muscles in general are very similar. I also included some thrushes and mimids as examples of somewhat more distant but not highly specialized forms. Altogether I believe that this collection of out-groups gives a good idea of the ancestral muscle forms in the general group from which the New World nine-primaried assemblage arose. It is in any event the best solution to the problem of out-group selection that available information and materials permitted.

MUSCLES OF THE FORELIMB

Detailed descriptions and illustrations of the forelimb muscles in a reference species, *Loxops virens*, were given previously (Raikow, 1977a). In the following section only variations from these conditions are given; where no variations are noted, the condition in all forms studied was as described for *Loxops*.

M. latissimus dorsi.—This muscle has two separate parts in most birds, and sometimes also includes cutaneous slips that are not considered in this study. Of the two main parts, pars cranialis occurs in all forms studied here. Pars caudalis is a parallel-fibered, strap-shaped muscle that arises from the neural spines of the dorsal vertebrae caudal to the origin of pars cranialis. It passes cranio-laterally to insert on the humerus deep to the insertion of pars cranialis. Pars caudalis is present in many nonpasserine orders as well as some families of passerines (George and Berger, 1966:293; Berger, 1969:220; Table 2) and, therefore, its absence in passeriformes is considered due to loss and is a derived state.

Pars caudalis occurs consistently in the Vireonidae, where it is present in all genera (Table 2). This supports the theory that the several genera are closely related, and set apart from the remainder of the assemblage. Among the Parulidae pars caudalis occurs only in *Peucedramus*, which supports the idea that the genus is misplaced in this family. Pars caudalis also occurs in a few species of Thraupidae and Icteridae, in some cases on one side of the body only (Table 1). This peculiar distribution could represent either the retention of a primitive state or its secondary reappearance (Raikow and Borecky, manuscript), but in view of its pattern of correlation with other myological characteristics, the latter explanation is more probable.

M. tensor propatagialis.—A scapular tendon (Raikow, 1977a) occurs in all members of the New World nine-primaried oscines (Fig. 1) except the

Vireonidae. It was also found in some Turdidae and Mimidae, but not other out-groups (Table 2). Its presence in the New World nine-primaried oscines may be primitive, or the structure could have arisen independently in the other forms. There is no compelling evidence allowing a choice of these alternatives. At any rate its absence does distinguish the Vireonidae from the other families.

M. deltoideus major.—In most forms the caudal head inserts fleshy. In *Psarocolius* (Icteridae) it narrows distally and inserts by a stout tendon. This appears to be an autapomorphic state in this genus only.

M. deltoideus minor.—This muscle arises from the pectoral girdle and inserts on the head of the humerus. In most cases the origin is from the scapula only, but sometimes there is also an origin from the adjacent coracoid. In the latter case the coracoidal origin may form a somewhat separate head, or a single continuous belly may be present. Because I suspect that the separation of the two heads may be an

Table 1.—Occurrence of *M. latissimus dorsi caudalis* in some species of Thraupidae and Icteridae.¹

Species	No. of specimens	Left side	Right side
Thraupidae			
<i>Thraupis virens</i>	7	+	+
<i>Thraupis palmarum</i>	2	+	+
<i>Thraupis palmarum</i>	1	—	+
<i>Thraupis cyanocephala</i>	3	—	—
Icteridae			
<i>Cacicus cela</i>	1	+	+
<i>Cacicus cela</i>	1	+	—
<i>Cacicus haemorrhous</i>	1	—	—
<i>Psarocolius angustifrons</i>	1	+	+
<i>Psarocolius decumanus</i>	1	—	—

¹ + = muscle present; — = muscle absent.

Table 2.—Major variations in pectoral musculature. For each muscle, the character states and character phylogenies are as follows: *M. latissimus dorsi pars caudalis*: + = present (primitive), - = absent (derived); *M. tensor propatagialis*, scapular tendon: + = present, - = absent (polarity undetermined); *M. deltoideus minor*, coracoidal head: + = present (derived), - = absent (primitive); *M. coracobrachialis cranialis*, + = well developed (primitive), ± = vestigial (derived), - = absent (further derived); *M. pronator profundus*: 1 = single belly (primitive), 2 = 2 bellies (derived); *M. flexor digitorum profundus*: 1 = belly wide (primitive), 2 = belly narrow (derived).

Species	M. latissimus dorsi pars caudalis	M. tensor propatagialis scapular tendon	M. deltoideus minor, coracoidal head	M. coraco- brachialis cranialis	M. pronator profundus	M. flexor digitorum profundus
Sylviidae						
<i>Sylvia atricapilla</i>	-	-	+	±	1	1
<i>Apalis flavida</i>	+	-	-	±	1	1
<i>Orthotomus atrogularis</i>	+	-	+	±	1	1
<i>Regulus satrapa</i>	-	?	-	±	1	1
Ploceidae/Estrildidae						
Grouped data on 41 genera from Bentz (1976). No. of genera indicated in paren- theses	+(29) -(12)	-(41)	+(4) -(37)	+(2) -(39)	1(32) 2(8)	?
Turdidae						
<i>Turdus migratorius</i>	+	?	-	±	1	2
<i>Sialia sialis</i>	-	+	-	-	1	2
<i>Catharus ustulatus</i>	+	+	-	-	2	2
Mimidae						
<i>Dumetella carolinensis</i>	+	+	-	±	2	1
Nectariniidae						
<i>Nectarinia sperata</i>	+	?	-	-	1	?
Vireonidae						
<i>Vireo olivaceus</i>	+	-	-	+	1	1
<i>Vireo pallans</i>	+	-	-	+	1	1
<i>Hylophilus poicilotis</i>	+	-	-	±	1	1
<i>Cyclarhis gujanensis</i>	+	-	-	±	1	1
<i>Vireolanus pulchellus</i>	+	-	-	+	1	1
Parulidae						
<i>Dendroica coronata</i>	-	+	-	-	2	1
<i>Geothlypis semiflava</i>	-	+	-	-	1	1
<i>Icteria virens</i>	-	+	+	-	2	1
<i>Mniotilta varia</i>	-	+	-	-	2	1
<i>Myioborus miniatus</i>	-	?	-	-	2	1
<i>Oporornis tolmei</i>	-	+	-	-	2	1
<i>Peucedramus taeniatus</i>	+	+	-	-	1	1
<i>Seiurus aurocapillus</i>	-	+	+	-	2	1
<i>Wilsonia pusilla</i>	-	+	-	-	2	1
<i>Basileuterus rufifrons</i>	-	+	-	-	1	1
Zeledoniidae						
<i>Zeledonia coronata</i>	-	+	-	+	1	1
Thraupidae						
<i>Sericossypha albocristata</i>	-	?	-	±	1	1
<i>Rhodinocichla rosea</i>	-	+	+	±	1	1
<i>Euphonia laniirostris</i>	-	+	-	±	1	1
<i>Tangara cyanicollis</i>	-	+	-	±	1	1
<i>Piranga ludoviciana</i>	-	+	-	±	2	1
<i>Rhamphocelus passerinii</i>	-	+	-	-	2	1

Table 2.—(Continued)

Species	M. latissimus dorsi pars caudalis	M. tensor propatagialis scapular tendon	M. deltoideus minor, coracoidal head	M. coraco- brachialis cranialis	M. pronator profundus	M. flexor digitorum profundus
<i>Tlraupis virens</i>	+	+	—	±	2	1
<i>Tachyphonus rufus</i>	—	+	—	±	2	1
<i>Urothraupis stolzmanni</i>	—	+	—	±	1-2	1
<i>Nephelornis oneilli</i>	—	+	—	±	1-2	1
			Tersinidae			
<i>Tersina viridis</i>	—	+	—	±	1	2
			Coerebidae			
<i>Conirostrum speciosum</i>	—	+	—	±	2	1
<i>Coereba flaveola</i>	—	+	—	?	2	1
<i>Dacnis cayana</i>	—	+	—	±	2	1
<i>Diglossa barbitula</i>	—	+	—	±	2	1
<i>Cyanerpes cyaneus</i>	—	+	—	?	2	1
<i>Chlorophanes spiza</i>	—	+	—	?	2	1
<i>Euneornis campestris</i>	—	+	—	±	2	1
			Catamblyrhynchidae			
<i>Catamblyrhynchus diadema</i>	—	+	—	+	2	1
			Fringillidae:Emberizinae			
<i>Aimophila ruficauda</i>	—	+	+	—	1	1
<i>Arremonops conirostris</i>	—	+	+	±	2	1
<i>Calcarius lapponicus</i>	—	+	+	—	2	1
<i>Chlorura chlorura</i>	—	+	+	—	2	1
<i>Emberiza flaviventris</i>	—	+	—	±	2	1
<i>Geospiza fuliginosa</i>	—	+	—	±	2	1
<i>Junco hyemalis</i>	—	+	+	±	2	1
<i>Loxigilla portoricensis</i>	—	?	—	±	2	1
<i>Passerella iliaca</i>	—	?	+	±	2	1
<i>Plectrophenax nivalis</i>	—	+	+	±	2	1
<i>Zonotrichia capensis</i>	—	+	+	—	2	1
			Fringillidae:Cardinalinae			
<i>Passerina cyanea</i>	—	+	—	±	2	1
<i>Pheucticus ludovicianus</i>	—	+	+	±	2	1
<i>Cardinalis cardinalis</i>	—	+	+	±	2	1
<i>Saltator maximus</i>	—	+	—	+	2	1
<i>Guiraca caerulea</i>	—	+	—	±	2	1
			Fringillidae:Carduelinae			
<i>Leucosticte australis</i>	—	+	+	?	?	1
<i>Leucosticte tephrocotis</i>	—	+	+	±	2	1
<i>Carpodacus cassinii</i>	—	+	—	?	2	1
<i>Pinicola enucleator</i>	—	+	+	±	2	1
<i>Serinus mozambicus</i>	?	+	?	?	?	1
<i>Serinus serinus</i>	—	+	+	±	2	1
<i>Carduelis carduelis</i>	—	+	+	?	2	1
<i>Chloris chloris</i>	—	+	+	±	2	1
<i>Hesperiphona vespertina</i>	—	+	+	±	2	1
<i>Loxia curvirostra</i>	—	+	+	±	2	1
<i>Pyrrhula pyrrhula</i>	—	+	+	±	2	1
<i>Carduelis pinus</i>	—	+	+	±	2	1
<i>Fringilla coelebs</i>	—	+	—	±	2	1

Table 2.—(Continued)

Species	M. latissimus dorsi pars caudalis	M. tensor propatagialis scapular tendon	M. deltoideus minor, coracoidal head	M. coraco- brachialis cranialis	M. pronator profundus	M. flexor digitorum profundus
Drepanididae						
<i>Hemignathus procerus</i>	—	+	+	—	2	1
<i>Hemignathus wilsoni</i>	—	?	+	?	2	1
<i>Paroreomyza maculata bairdi</i>	—	?	+	±	2	1
<i>Loxops virens wilsoni</i>	—	+	+	±	2	1
<i>Psittirostra cantans cantans</i>	—	+	+	±	2	1
<i>Psittirostra cantans ultima</i>	—	+	+	?	2	1
<i>Psittirostra psittacea</i>	—	+	+	±	2	1
<i>Himatione sanguinea</i>	—	+	+	?	2	1
<i>Vestiaria coccinea</i>	—	+	+	±	2	1
<i>Palmeria dolei</i>	—	+	+	±	2	1
Icteridae						
<i>Cacicus cela</i>	+	+	—	±	1	2
<i>Cassiculus melanicterus</i>	—	+	—	±	2	2
<i>Dolichonyx oryzivorus</i>	—	+	+	±	2	2
<i>Psarocolius decumanus</i>	—	+	—	±	1	2
<i>Quiscalus quiscula</i>	—	+	+	±	2	2
<i>Spiza americana</i>	—	+	+	±	2	2
<i>Sturnella magna</i>	—	+	+	±	2	2
<i>Sturnella neglecta</i>	—	+	?	?	?	2
<i>Agelaius phoeniceus</i>	—	+	+	±	2	2
<i>Icterus parisorum</i>	—	+	—	±	2	2
<i>Molothrus ater</i>	—	+	+	±	2	2

artifact resulting from manipulation, I have not distinguished these variants. The significant variation in this muscle, therefore, is the presence or absence of a coracoidal head. I have described and illustrated this variation previously (Raikow, 1977b). A coracoidal head is absent in most out-groups and in most New World nine-primaried oscines, including the generally primitive Vireonidae and most Parulidae. For these reasons its absence is considered primitive and its presence derived in the assemblage under investigation.

The only groups in which a coracoidal head is virtually universal are the Carduelinae and Drepanididae, which argues for their close relationship (Raikow, 1977b). In the Parulidae it occurs only in *Icteria*, whose position in the family is uncertain, and in *Seiurus*, which is also aberrant in some hind-limb muscles. Among the Emberizinae the coracoidal head is absent only in a few genera. In the Thraupidae the coracoidal head is absent, but the scapular head is relatively slender, which is apparently also a derived state. In *Saltator* and *Catamblyrhynchus* the muscle is also slender, supporting their connection to this family. On the other hand, the peculiar

Rhodinocichla, which is currently included in the Thraupidae with uncertainty, possesses a coracoidal head. See Table 2.

M. coracobrachialis cranialis.—This is a small (ca. 3-mm long) parallel-fibered muscle of the shoulder. It arises from the cranial surface of the head of the coracoid and inserts on the humerus between the articular surface and the pectoralis insertion. The muscle is buried in the tissue of the coracohumeral joint capsule, which must be dissected away to reveal the tiny belly (Fig. 2). It is well developed in *Vireo* and *Vireolanus*, but in *Hylophilus* and *Cyclarhis* it is pale in color and takes up little or no stain as compared to normal muscles. It arises by a well-defined tendon, but the belly is soft and difficult to separate from surrounding connective tissue, though slightly more dense than the latter. This appears to be a degenerate condition, with perhaps an absence or poor development of muscle fibers, which may be partly or mostly replaced by connective tissue. This would have to be determined by histological examination. In any event I term this condition vestigial, as it appears to represent a stage leading to complete loss. The muscle is well developed in *Zeledonia*,

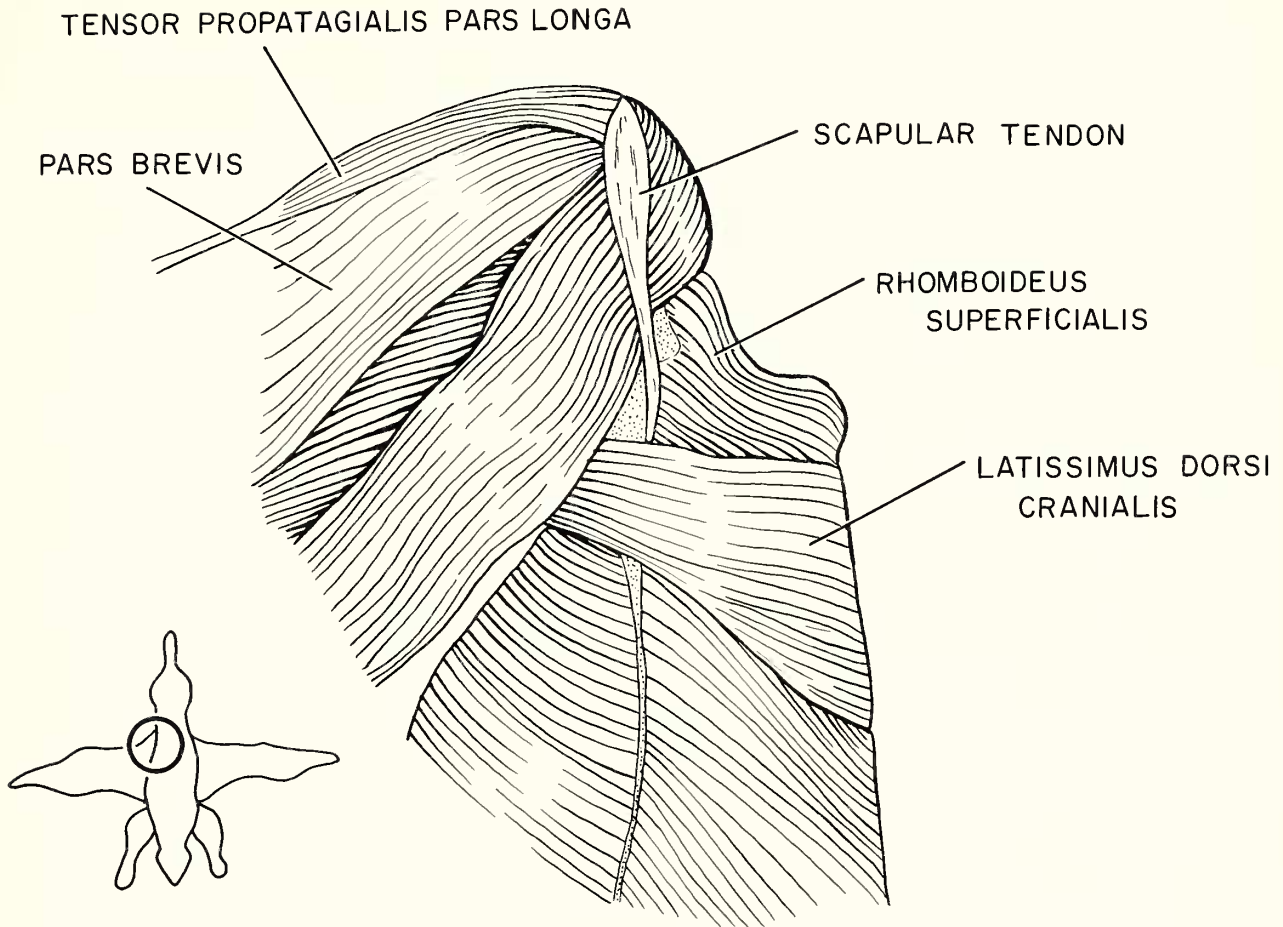


Fig. 1.—Dorsal view of the superficial muscles of the shoulder in *Hesperiphona vespertina* showing the scapular tendon passing from the origin of the two parts of *M. tensor propatagialis* to the dorsal surface of the scapula.

staining deeply. It is apparently absent in Parulidae, where I could find no trace. It is present in *Saltator* and *Catamblyrhynchus*. Otherwise it is demonstrable in most other forms as a vestige, or not at all, especially in smaller species.

This muscle is present in many nonpasserine orders (George and Berger, 1966:313–315); hence its reduction and loss are a derived trend in the group studied. Its relative retention in *Zeledonia* and *Catamblyrhynchus* set these forms apart as primitive offshoots of the Parulidae and Thraupidae, respectively, with which they are currently associated.

M. serratus superficialis.—In *Catamblyrhynchus* the caudal head of pars cranialis is wider than usual, arising not only from the first true rib (and its unciniate process) but also from the second true rib. Pars costohumeralis generally arises from the third true rib, but from the fourth in *Tangara* and *Tersina*.

M. rhomboideus superficialis.—In most cases this muscle inserts only on the scapula, but in a few cases the area of insertion is extended cranially so that a few fascicles also insert on the clavicle. This insertion is on the medial surface of the head of the clavicle and the shaft just distal to the head. It occurs in *Sialia*, *Nectarinia*, and to a small extent in *Quiscalus*. In *Zonotrichia*, *Chlorura*, and *Emberiza*, in contrast, the muscle is shorter, its anterior extreme ending about 2 mm short of the clavicle.

M. serratus profundus.—In most cases the cranial head arises by two slips, one each from the penultimate and antepenultimate cervical vertebrae. An origin from only the penultimate vertebra was found in *Wilsonia*, *Loxops*, and *Himatione*.

M. expansor secundariorum.—In *Rhodinocichla* this inserts only on the proximal two secondaries, rather than three as in most species.

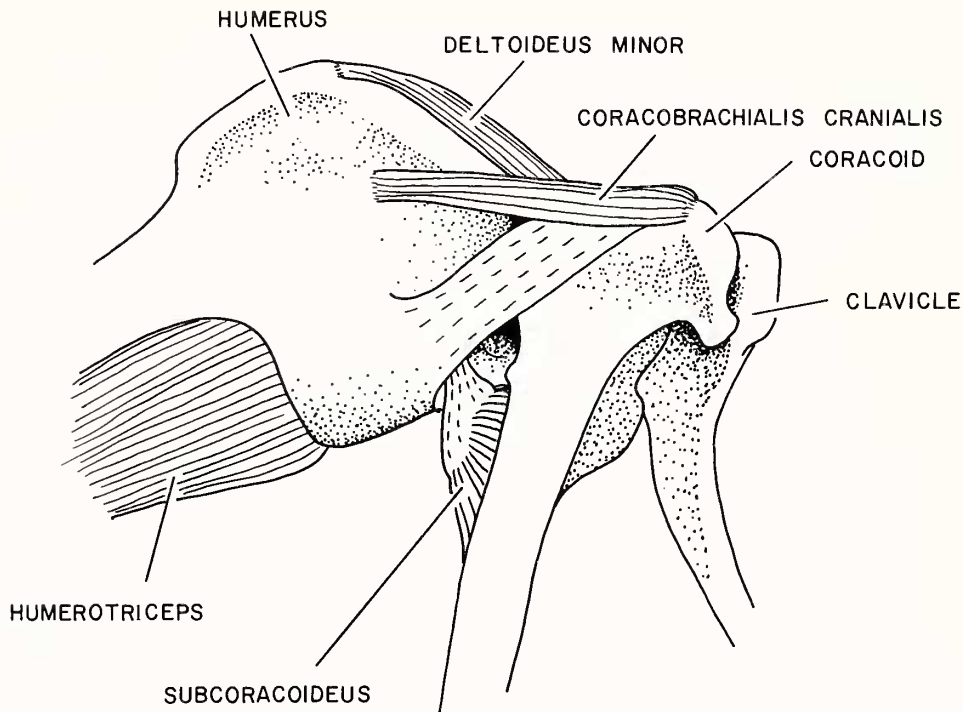


Fig. 2.—Deep shoulder muscles in *Vireolanius pulchellus* showing the well-developed coracobrachialis cranialis muscle.

M. pronator profundus.—As noted by Berger (1969:221), this muscle arises in part by a tendon from the humerus and in part fleshy from the adjacent humeroulnar pulley. These two parts tend to form separate bellies, but there is a distinct variation in the degree of separation in the bellies (Fig. 3). In Type 1 the two parts are adjacent and more or less fused together, so that the belly is essentially single, flat, and fan shaped. It spreads out to an essentially continuous line of insertion along the radius. In Type 2, however, the two bellies become separated. The proximal belly inserts proximally on the radius by a flat aponeurosis, while the distal belly inserts more distally on the radius by a narrow tendon that arises along its cranial surface. Between these two bellies there stretches a very thin connective tissue membrane that may represent a vestige of the formerly continuous tendon of insertion, but has no mechanical strength in this form, and indeed may merely be derived from fascia. The effect of this change is to make two distinct muscular bellies rather than one, presumably with a capability of acting more independently of each other in contraction, and thus increasing the functional versatility of the pronator profundus.

In their review of this muscle, George and Berger (1966:346–347) did not mention a separation of this muscle into two bellies in nonpasserine birds. Most other passerines studied have Type 1, but a few have Type 2. This suggests that the separation into two bellies (Type 2) is a derived state in passerines, probably arising several times (Table 2).

M. flexor digitorum profundus.—In all Icteridae examined (including *Spiza*) this muscle narrows distally so that its caudal margin does not overlie the distal part of the belly of the underlying *M. ulnometacarpalis ventralis* (Fig. 4). A similar condition was seen only in *Tersina*, among the New World nine-primaried oscines (Table 2).

M. extensor digitorum communis.—In *Tersina* the belly is longer than usual, extending nearly the entire length of the ulna.

M. interosseus dorsalis.—In *Zeledonia* the belly was lacking, the fine tendon being anchored in connective tissue. In *Catamblyrhynchus* the belly is reduced to a tiny vestige, the tendon still being present.

M. ulnometacarpalis ventralis.—This muscle arises from the ulna, and may have one or two moderately separate heads. The two-headed condition may simply represent a v-shaped origin of the single bel-

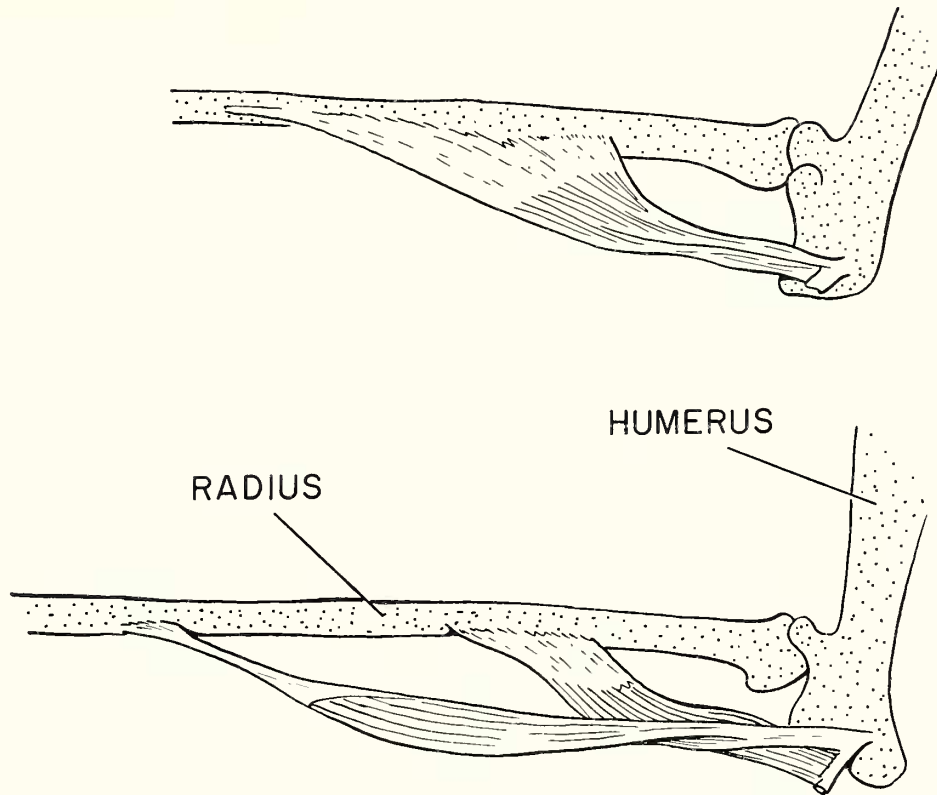


Fig. 3.—Variation in *M. pronator profundus*. Above, the primitive Type 1 with a continuous belly, shown in *Vireo olivaceus*. Below, the derived Type 2 with separate bellies, shown in *Dolichonyx oryzivorus*.

ly, however, distinctly separate heads being unusual. Most forms studied have the v-shaped origin, but some members of most families have the single condition, which occurs most consistently in the Drep-

anididae. Although Berger (1968:221) suggested that this variation might prove taxonomically useful, the extent of intergradation and apparently random distribution make it of no value in the present study.

MUSCLES OF THE HINDLIMB

Detailed descriptions and illustrations of the hindlimb muscles have been given previously (Raikow, 1976) for the reference species *Loxops virens*. In the following section I report variations in some of these muscles; where no variations are noted, the muscle in all forms examined was like that in *L. virens*. There are also some comments related to muscle variations in passerines generally, which will add to the review given by Berger (1969).

M. iliotibialis lateralis.—In some passerines the postacetabular portion of the muscle is absent (Berger, 1969:221) but both pre- and postacetabular portions were present in the New World nine-primaried

oscines. Stallcup (1954:165) reported that in *Vireo* the muscle lacks a central aponeurotic portion found in other forms, but I found it present and identical to the condition in the other species, including some that Stallcup also dissected. In *Sericossypha* a small part of the dorsal fleshy part is absent between the pre- and postacetabular parts, and reaching as far distally as the distal central aponeurosis of the muscle.

M. femorotibialis externus.—No differences were noted. Berger (1969:221) reported a deep distal head in some passerines, which I also described in *L. virens*. Because Berger did not name these divisions,

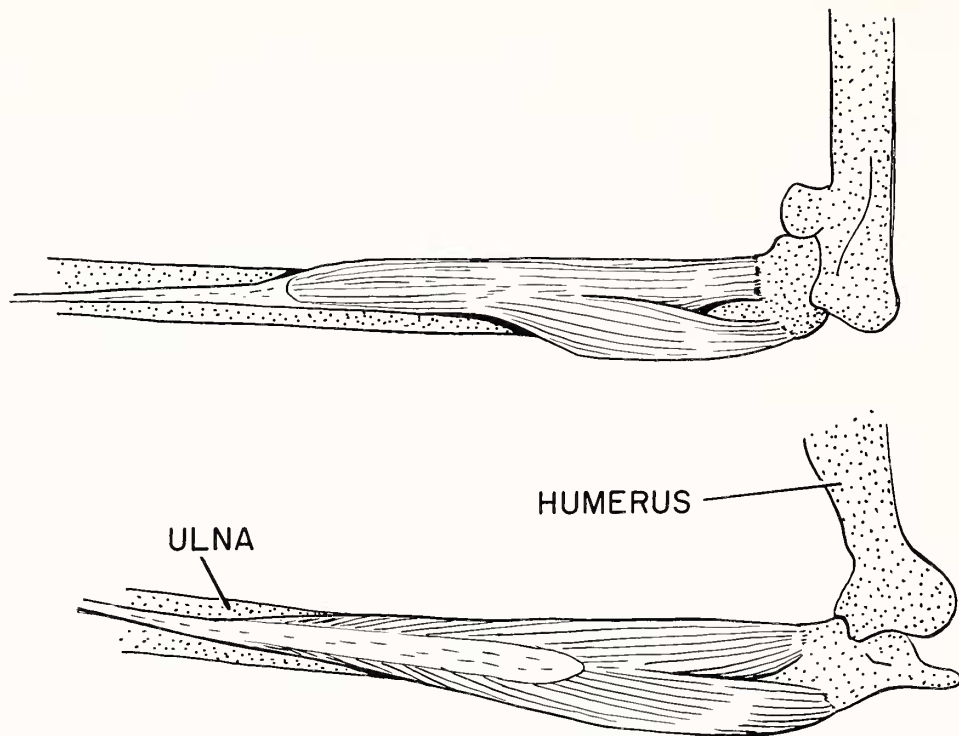


Fig. 4.—Variation in *M. flexor digitorum profundus*. Above, the derived state with narrowed distal portion of the belly, shown in *Spiza americana*. Below, the primitive state in *Sericossypha albocristata*.

I propose the terms *pars proximalis* (the superficial part) and *pars distalis* (the deep, distal head). Stallcup (1954) did not describe *pars distalis*, but apparently overlooked it as I found it in many species that he studied. I also found it in *Hirundo* (it was not mentioned by Gaunt, 1969), and in some Sturnidae, Mimidae, Corvidae, Turdidae, Alaudidae, Paridae, and Nectariniidae. The division of *M. femortibialis externus* into proximal and distal heads is probably common in passerines but has been overlooked by most workers.

M. pubo-ischiofemoralis.—Gaunt (1969) found that *pars cranialis* and *pars caudalis* are fused together in the Hirundinidae, but they are separate in the forms studied here. Stallcup (1954:168) claimed that the origin is modified in *Vireo*, but I could not find any difference from the other forms examined.

M. obturatorius lateralis.—This muscle has distinct dorsal and ventral bellies (Fig. 5). *Pars ventralis* is present in all forms studied, but *pars dorsalis* is absent in some. Because it occurs in many groups of birds, its absence in some genera of the families studied herein is undoubtedly due to loss and is derived. When present, *pars dorsalis* varies in size. I term it

small when the area of origin is not caudal to the obturator foramen; medium when the origin lies between the obturator foramen and the midpoint of the ilioischiatric fenestra; and large when the origin lies caudal to this point. *Pars dorsalis* is large in most families studied herein, and in most of the out-groups as well. Thus its reduction in size in the Carduelinae and Drepanididae must be a derived state, and one that supports the theory (Raikow, 1977b) that these families are sister groups. Reduction continues to a point of complete loss in some cardueline genera. The *pars dorsalis* is also independently lost in a few genera of families where it is otherwise well developed (Table 3). Bentz (1976) found a similar tendency toward loss in the Old World finches.

M. gastrocnemius.—This muscle has three separate bellies with a common tendon of insertion. *Pars externa* and *pars intermedia* do not vary, but *pars interna* is highly variable and of some taxonomic use (Fig. 6). *Pars interna* is the most superficial muscle on the medial surface of the crus, arising by two distinct heads. The superficial head arises in part from the inner cnemial crest of the tibiotarsus, while a band of fibers (the patellar band) may extend around

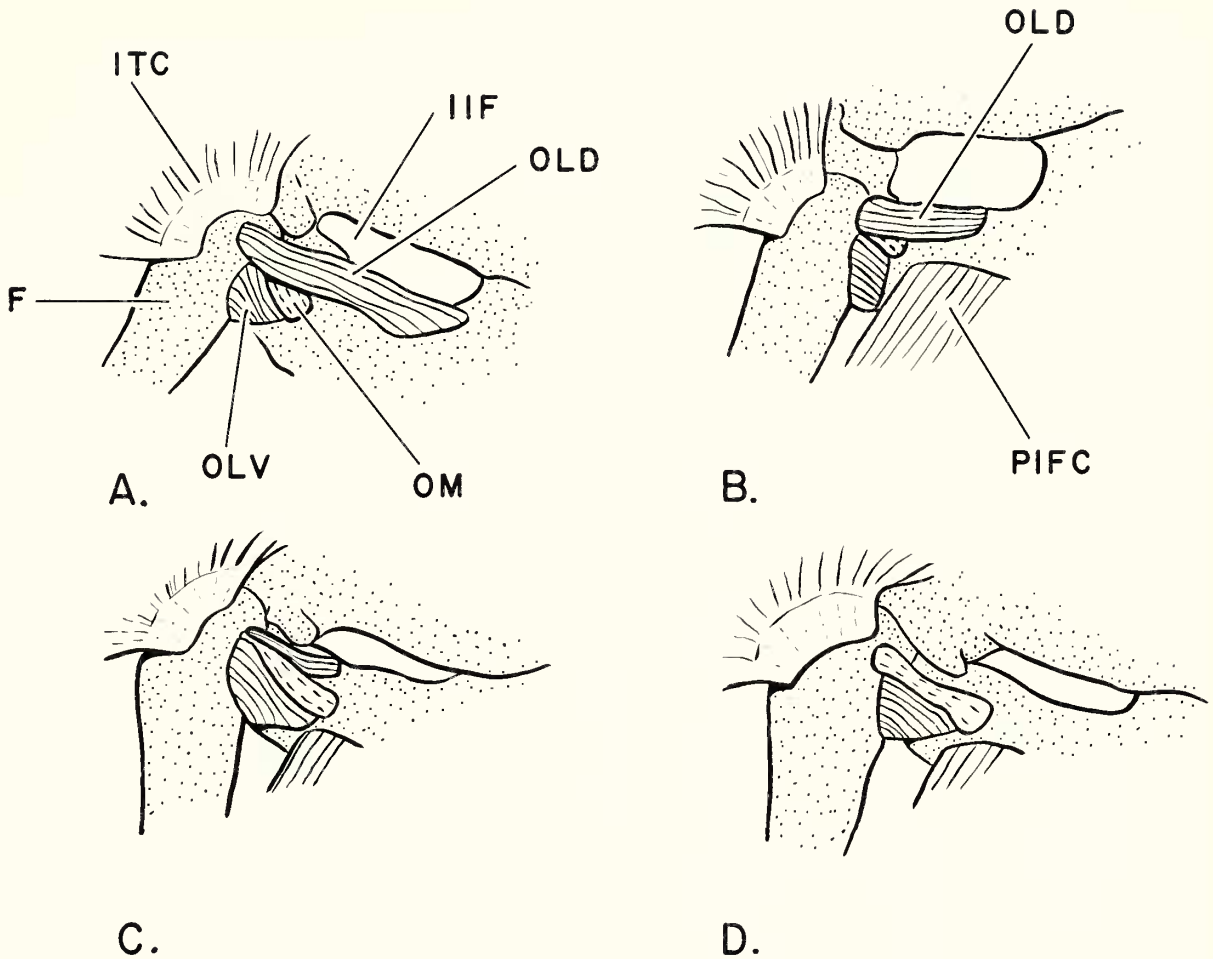


Fig. 5.—Deep muscles of the hip in four species of New-World, nine-primaried oscines, showing variation in the size and occurrence of *M. obturatorius lateralis pars dorsalis*. A) *Cyanerpes cyaneus*, showing muscle of large size; B) *Loxops virens wilsoni*, showing muscle of medium to large size; C) *Pinicola enucleator*, showing muscle of small size; D) *Hesperiphona vespertina*, showing muscle absent. Abbreviations: F, femur; IIF, ilio-ischiatic fenestra; ITC, *M. iliio-trochanterichus caudalis*; OLD, *M. obturatorius lateralis pars dorsalis*; OLV, *M. obturatorius lateralis pars ventralis*; OM, tendon of *M. obturatorius medialis*; PIFC, *M. pubo-ischiofemorialis pars cranialis*.

the knee, arising from the patellar tendon. The deep head of *pars interna* arises from the medial surface of the head of the tibiotarsus. The two heads fuse and the common belly extends caudally. Stallcup (1954) noted some variation in *pars interna*, but a more detailed classification of this variation is given here. In Type 1 the superficial head is present, including a patellar band. In Type 2 the superficial head is present but lacks a patellar band. In Type 3 the superficial head is absent. In forms having Type 1 the relative size of the patellar band varies. This is expressed in Table 3 as the percentage of the distance between the patellar crest and the patella which the origin of the patellar band covers (Fig. 7). This vari-

ation is only of occasional usefulness, but variation in the Types 1 through 3 is more valuable taxonomically. The three types appear to be stages in a morphocline. I believe that Type 1 is the ancestral state in the New World nine-primaried oscines because of out-group comparisons (Table 3), because it is the most common condition within the group, and because it occurs in families (for example, Parulidae) generally considered on other grounds to be primitive within the assemblage.

The derived state, loss of the patellar band, occurs in some cardinalines and thraupids, most carduelines, and all icterids. If this were considered a synapomorphy, however, it would conflict with oth-

Table 3.—Major variations in pelvic musculature. For each muscle, the character states and character phylogenies are as follows: *M. gastrocnemius pars interna*: 1 = superficial head present, including patellar band (primitive), 2 = superficial head present but patellar band absent (derived), 3 = superficial head absent (further derived); Patellar band: decimal value = width of band as % of distance between patella and patellar crest (polarity undetermined); *M. obturatorius lateralis pars dorsalis*: - = absent (derived), size classes defined in text (polarity undetermined); *M. plantaris*: + = present (primitive), - = absent (derived); *M. peroneus brevis tibial head*: - = absent (primitive), ± = partially developed (derived), + = fully developed (further derived); *M. flexor digitorum longus*: ABB (primitive), other patterns (derived).

Species	M. gastrocnemius pars interna	Patellar band	M. obturatorius lateralis pars dorsalis	M. plantaris	M. peroneus brevis tibial head	M. flexor digitorum longus
Sylviidae						
<i>Sylvia atricapilla</i>	1	0.95	lge.	+	-	ABB
<i>Apalis flavida</i>	1	0.80	lge.	+	-	ABB
<i>Orthotomus atrogularis</i>	1	1.00	lge.	+	-	ABB
<i>Regulus satrapa</i>	1	0.60	lge.	-	+	ABB
Ploceidae/Estrildidae						
Grouped data on 41 genera from Bentz (1976). No. of genera indicated in parentheses. Some genera have more than one condition in different species.	1(7) 2(30) 3(8)	0-1.00	-(26) sml.(10) med.(5) lge.(3)	+(37) -(4)	-(41)	ABB(37) ABC(3) AAA(1)
Turdidae						
<i>Turdus migratorius</i>	1	0.50	lge.	+	-	ABB
<i>Sialia sialis</i>	1	0.50	lge.	+	-	ABB
<i>Catharus ustulatus</i>	1	0.80	lge.	+	-	ABB
Mimidae						
<i>Dumetella carolinensis</i>	1	1.00	lge.	+	-	ABB
Nectariniidae						
<i>Nectarinia sperata</i>	1	0.50	lge.	+	-	AAB
Vireonidae						
<i>Vireo olivaceus</i>	1	0.70	med.	+	-	AAB
<i>Vireo pallens</i>	1	0.90	lge.	+	-	AAB
<i>Hylophilus poicilotis</i>	1	0.80	med.	+	-	AAB
<i>Cyclarhis gujanensis</i>	1	0.30	med.	+	-	AAB
<i>Vireolanius pulchellus</i>	1	1.00	sml.	+	-	AAB
Parulidae						
<i>Dendroica coronata</i>	1	0.70	med.	+	-	ABB
<i>Geothlypis semiflava</i>	1	0.50	lge.	+	-	ABB
<i>Icteria virens</i>	1	0.90	med.	+	-	ABB
<i>Mniotilta varia</i>	1	0.80	med.	+	-	ABB
<i>Myioborus miniatus</i>	1	0.80	med.	+	-	ABB
<i>Oporornis tolmiei</i>	1	0.90	med.	+	-	ABB
<i>Peucedramus taeniatus</i>	1	0.90	lge.	+	-	ABB
<i>Seiurus aurocapillus</i>	1	0.90	-	+	+	ABB
<i>Wilsonia pusilla</i>	1	1.00	med.	+	-	ABB
<i>Basileuteurus rufifrons</i>	1	1.00	med.	+	-	ABB
Zeledoniidae						
<i>Zeledonia coronata</i>	1	1.00	med.	+	-	ABB
Thraupidae						
<i>Sericossypha albocristata</i>	2	-	med.-lge.	+	±	ACB
<i>Rhodinocichla rosea</i>	1	0.60	lge.	+	-	CBB
<i>Euphonia laniirostris</i>	1	0.50	med.	+	-	ABB
<i>Tangara cyanicollis</i>	1	0.60	med.	+	±	ABB
<i>Piranga ludoviciana</i>	2	-	med.	+	-	ABB

Table 3.—(Continued)

Species	M. gastro- cnemius pars interna	Patellar band	M. obturatorius lateralis pars dorsalis	M. plantaris	M. peroneus brevis tibial head	M. flexor digitorum longus
<i>Rhamphocelus passerini</i>	2	—	med.	+	—	ABB
<i>Thraupis virens</i>	2	—	lge.	+	—	ABB
<i>Tachyphonus rufus</i>	3	—	lge.	+	—	ABB
<i>Urothraupis stolzmanni</i>	1	0.80	lge.	+	±	ABA
<i>Nephelornis oneilli</i>	1	0.80	lge.	+	±	ABB
Tersinidae						
<i>Tersina viridis</i>	3	—	med.	+	—	ACB
Coerebidae						
<i>Conirostrum speciosum</i>	1	0.40	med.	+	—	ABB
<i>Coereba flaveola</i>	1	1.00	lge.	+	±	ABB
<i>Dacnis cayana</i>	1	0.40	med.	+	—	ABB
<i>Diglossa barbitula</i>	1	1.00	lge.	—	—	ABB
<i>Cyanerpes cyaneus</i>	3	—	lge.	—	—	ABB
<i>Chlorophanes spiza</i>	1	0.30	lge.	+	—	ACB
<i>Euneornis campestris</i>	1	0.80	lge.	+	—	ABB
Catamblyrhynchidae						
<i>Catamblyrhynchus diadema</i>	1	1.00	lge.	—	—	ABA
Fringillidae: Emberizinae						
<i>Aimophila ruficauda</i>	1	0.60	lge.	+	—	ABB
<i>Arremonops conirostris</i>	1	1.00	med.	+	—	ABB
<i>Calcarius lapponicus</i>	1	0.70	med.	+	—	BBB
<i>Chlorura chlorura</i>	1	1.00	?	+	—	ABB
<i>Emberiza flaviventris</i>	1	0.40	lge.	+	—	?
<i>Geospiza fuliginosa</i>	1	1.00	lge.	+	—	ABB
<i>Junco hyemalis</i>	1	1.00	lge.	+	—	BBB
<i>Loxigilla portoricensis</i>	1	0.60	lge.	+	—	ABB
<i>Passerella iliaca</i>	1	0.80	lge.	+	—	BBB
<i>Plectrophenax nivalis</i>	1	0.30	lge.	+	—	?
<i>Zonotrichia capensis</i>	1	0.70	med.	+	—	ABB
Fringillidae: Cardinalinae						
<i>Passerina cyanea</i>	2	—	lge.	+	—	ABB
<i>Pheucticus ludovicianus</i>	3	—	lge.	+	—	ABB
<i>Cardinalis cardinalis</i>	1	0.25	lge.	+	—	ABB
<i>Saltator maximus</i>	1	0.25	sml.	+	—	ABB
<i>Guiraca caerulea</i>	2	—	lge.	+	—	AAB
Fringillidae: Carduelinae						
<i>Leucosticte australis</i>	1	0.70	sml.	+	—	BBB
<i>Leucosticte tephrocotis</i>	1	0.60	—	+	—	ABB
<i>Carpodacus cassini</i>	2	—	sml.	—	—	ABB
<i>Pinicola enucleator</i>	2	—	sml.	+	—	ABB
<i>Serinus mozambicus</i>	2	—	med.	+	±	ABB
<i>Serinus serinus</i>	2	—	sml.	—	±	?
<i>Carduelis carduelis</i>	3	—	med.	—	+	ABB
<i>Chloris chloris</i>	3	—	—	+	+	ABB
<i>Hesperiphona vespertina</i>	3	—	—	+	—	ABC
<i>Loxia curvirostris</i>	3	—	sml.	—	+	ABB
<i>Pyrrhula pyrrhula</i>	3	—	—	+	+	ABB
<i>Carduelis pinus</i>	3	—	sml.	—	+	ABB
<i>Fringilla coelebs</i>	3	—	sml.	+	—	ABB

Table 3.—(Continued)

Species	M. gastrocnemius pars interna	Patellar band	M. obturatorius lateralis pars dorsalis	M. plantaris	M. peroneus brevis tibial head	M. flexor digitorum longus
Drepanididae						
<i>Hemignathus procerus</i>	1	0.75	med.	+	+	ABB
<i>Hemignathus wilsoni</i>	1	0.60	sml.	+	+	ABB
<i>Paroreomyza maculata bairdi</i>	1	0.60	sml.	+	+	ABB
<i>Loxops virens wilsoni</i>	1	0.75	med.	—	+	ABB
<i>Psittirostra cantans cantans</i>	1	0.50	sml.	+	+	ABA
<i>Psittirostra cantans ultima</i>	1	0.50	sml.	+	+	ABA
<i>Psittirostra psittacea</i>	1	0.40	sml.	+	+	ABB
<i>Himatione sanguinea</i>	1	0.60	med.	—	+	ABB
<i>Vestiaria coccinea</i>	1	0.70	sml.	—	+	ABB
<i>Palmeria dolei</i>	1	0.75	med.	—	+	ABA
<i>Ciridops anna</i>	1	>0.50	med.	?	?	?
Icteridae						
<i>Cacicus cela</i>	2	—	lge.	+	—	ABA
<i>Cassiculus melanicterus</i>	2	—	med.	+	—	ABB
<i>Dolichonyx oryzivorus</i>	2	—	med.	+	—	ABB
<i>Psarocolius decumanus</i>	2	—	lge.	+	—	ABB
<i>Quiscalus quiscula</i>	2	—	lge.	+	—	ABB
<i>Spiza americana</i>	2	—	med.	+	—	ABB
<i>Sturnella magna</i>	2	—	—	+	—	ABA
<i>Sturnella neglecta</i>	2	—	?	+	?	?
<i>Agelaius phoeniceus</i>	3	—	lge.	+	—	ABA
<i>Icterus parisorum</i>	3	—	med.	+	—	ABB
<i>Molothrus ater</i>	3	—	med.	+	—	ABB

* Reduced.

er data as discussed below, so most probably the loss of the patellar band has occurred independently in these three groups.

M. peroneus brevis.—This muscle shows an important variation not previously described in birds. In most forms studied it arises from the fibula alone, or also the adjacent tibial shaft. In some, however, there is also a fleshy origin from the caudal margin of the lateral cnemial crest, just caudal to the origin of the tibial head of *M. tibialis cranialis*. This *tibial head* passes distad superficial to the femoral head of the *tibialis cranialis*, and joins the usual fibular head to form a single belly. I have illustrated this muscle and discussed its mode of origin elsewhere (Raikow, 1977b). Its occurrence is listed in Table 3. Because it does not occur in other birds so far as known, and because it is found here in the carduelines and drepanidids, two groups of advanced position in the New World nine-primaried assemblage, the presence of a tibial head is clearly derived and argues for a sister-group relationship of these two families (Raikow, 1977b). A partial or complete tib-

ial head was also found in a few other genera (Table 3) where it presumably arose independently.

M. flexor perforatus digiti II.—In *Rhodinocichla rosea* the muscle was distinct, having a small secondary head originating from the surface of *M. flexor hallucis longus*, and joining the main head along its medial border. This condition was not observed in any other form. Berger (1969:222) reported that the tendon of insertion in this muscle is not perforated by the tendons of *M. flexor perforans et perforatus digiti II* or *M. flexor digitorum longus* in various passerines. Stallcup (1954:171) claimed that it is so perforated in the species he studied. I believe that in all the species I studied the tendon is not perforated, and that Stallcup made an error in interpretation. It appears from his description of the insertion, when compared to observation of specimens, that what he considered a sheathlike termination of the tendon of *M. flexor perforatus digiti II* is actually the tendon sheath of the first phalanx. Although this is in contact with the tendon of *M. flexor perforatus digiti II* at its insertion, the sheath

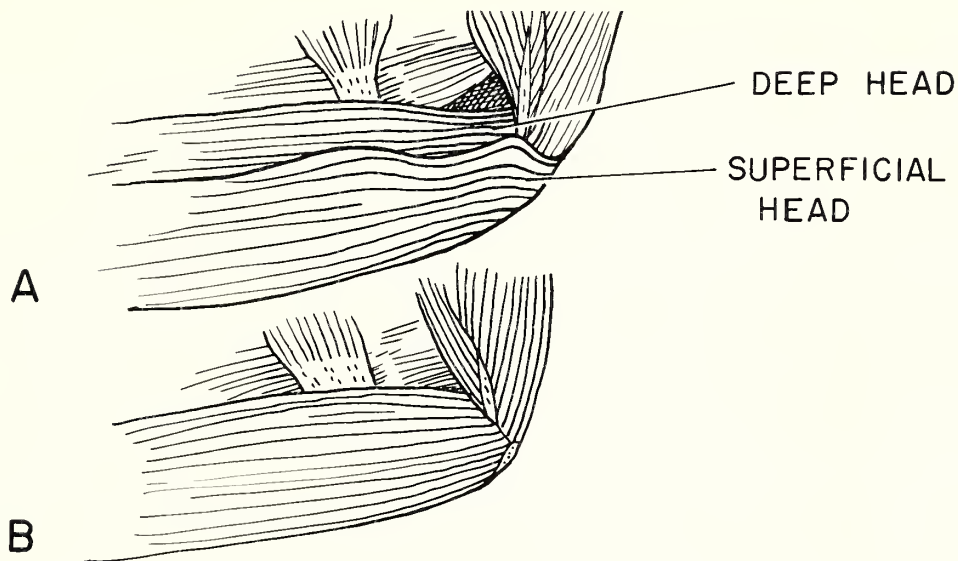


Fig. 6.—Medial view of the knee area showing variation in *M. gastrocnemius pars interna*. A) *Sericossypha albocristata*, showing the superficial head present as in Types 1 and 2. B) *Icterus parisorum*, showing Type 3 with the superficial head lacking.

itself should not be considered part of that tendon. Such a sheath covers all the flexor tendons on the plantar surface of each phalanx of every digit. Stallcup (1954:171) stated that this muscle is not in contact with *M. flexor hallucis longus* in *Vireo*, but I found that it is in such contact as in the other species studied.

M. plantaris.—This muscle is designated by the letter F in muscle formulae, and until recently was considered present in all passerines. However, Gaunt (1969) found it absent in most Hirundinidae, and Bentz (1976) in some estrildids. I also found it absent in some New World nine-primaried oscines (Table 3). Because *M. plantaris* is present in many passerine and nonpasserine families, its absence here is considered a derived state due to loss.

M. flexor hallucis longus.—Berger (1969:22) noted that the muscle may have one, two, or three heads of origin in passerines. Stallcup (1954:174) reported the lateral head absent in *Vireo*, but I found it present. According to Stallcup (1954) the usual origin is by two heads, but Berger found three heads in *Agelaius* (George and Berger, 1966:443) and *Dendroica* (Berger, 1968:613). My findings agree with Berger's descriptions, and it appears that Stallcup failed to distinguish between the intermediate and medial heads described by Berger.

M. flexor digitorum longus.—There is a third, femoral head of origin in some birds. Among the

forms included in this study, a femoral head was found only in the tanager *Sericossypha*, arising from the lateral condyle of the femur and passing caudad to join the fibular head. The tendon of this muscle divides into three branches inserting on the three anterior digits. Variations in this pattern of insertion (Fig. 8; Table 3) are sufficiently constant in recognized groups to be useful in this study. The usual pattern in the New World nine-primaried oscines is ABB (letter designations are shown in Fig. 8), the main exception being the Vireonidae with AAB. In other families there are occasional variations, usually involving the addition of delicate accessory vincula, but only in the Vireonidae is the variation consistent. It is difficult to determine the polarity of this character as the structural changes involved are minor, but out-group comparisons (Table 3) suggest that ABB is probably primitive.

M. flexor hallucis brevis.—In the Vireonidae this muscle is greatly enlarged and somewhat bipennate in structure, while in most groups it is quite small (or even apparently absent) and appears to be narrowly fan-shaped (Fig. 9). This sets the Vireonidae apart from the New World nine-primaried oscines, and also clusters the four genera of the Vireonidae, attesting to the unity of the group. The large size is probably a derived specialization of the Vireonidae as it did not occur in other groups studied.

M. extensor hallucis longus.—This muscle con-

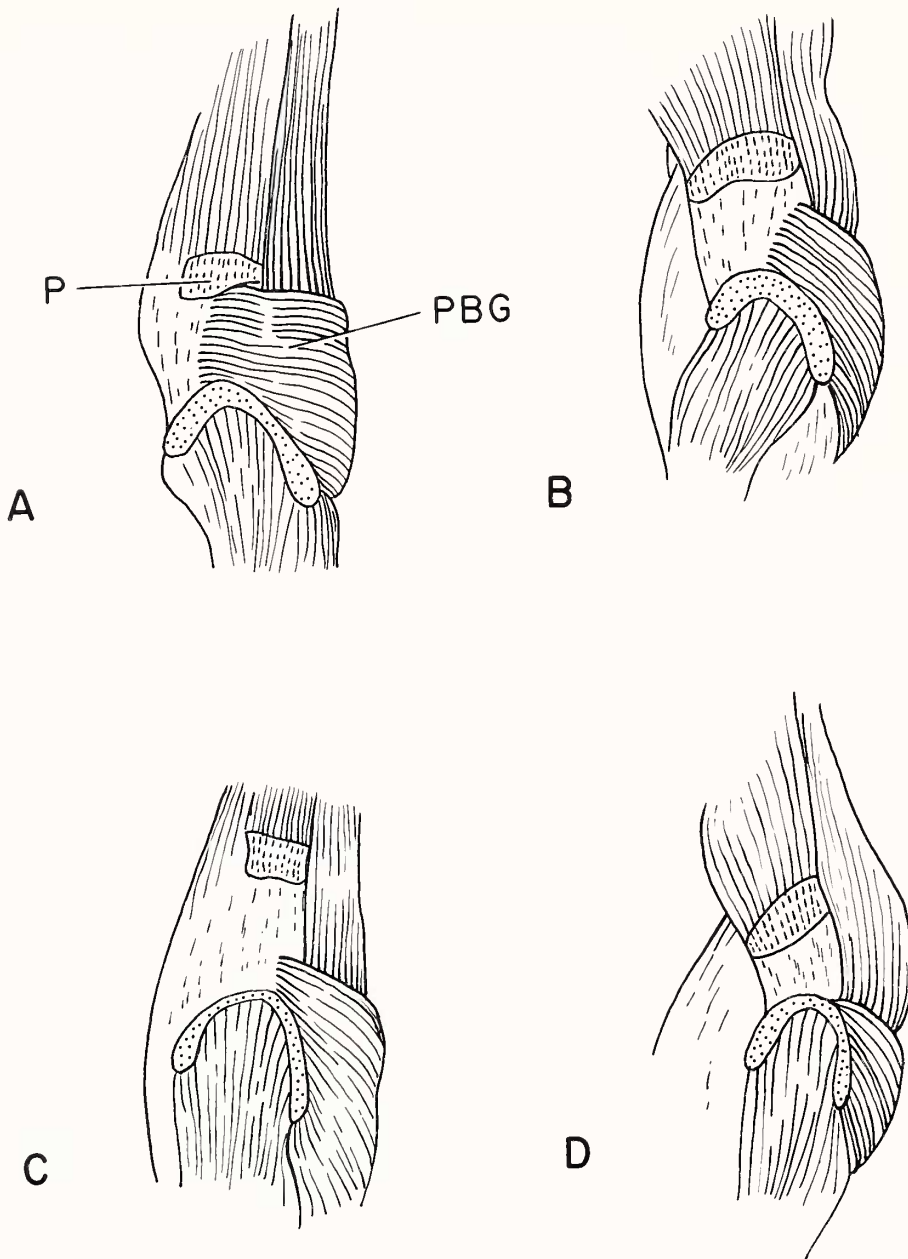


Fig. 7.—Cranial view of the knee in four species showing variation in the size and occurrence of the patellar band of *M. gastrocnemius* pars interna. A) *Coereba flaveola*, Type 1, patellar band size 1.00; B) *Leucosticte tephrocotis*, Type 1, patellar band size 0.60; C) *Saltator maximus*, Type 1, patellar band size 0.25; D) *Carpodacus cassini*, Type 2, patellar band absent. See text for explanation. Abbreviations: P, patella; PBG, patellar band of *M. gastrocnemius*.

sists of proximal and distal heads. The proximal head is as described by Berger (1968). A distal head has been described in a few nonpasserine birds (George and Berger, 1966:454–455), but apparently has not previously been found in passerines. It can be demonstrated only under high magnification (25×) and with the iodine stain. It is a fan-shaped

muscle about 3 mm long, and arises from the medial surface of the distal end of the shaft of the tarsometatarsus just proximal to the first metatarsal. It passes distad alongside the tendon of the proximal head and inserts into the joint capsule between metatarsal I and the proximal phalanx of the hallux (Fig. 9).

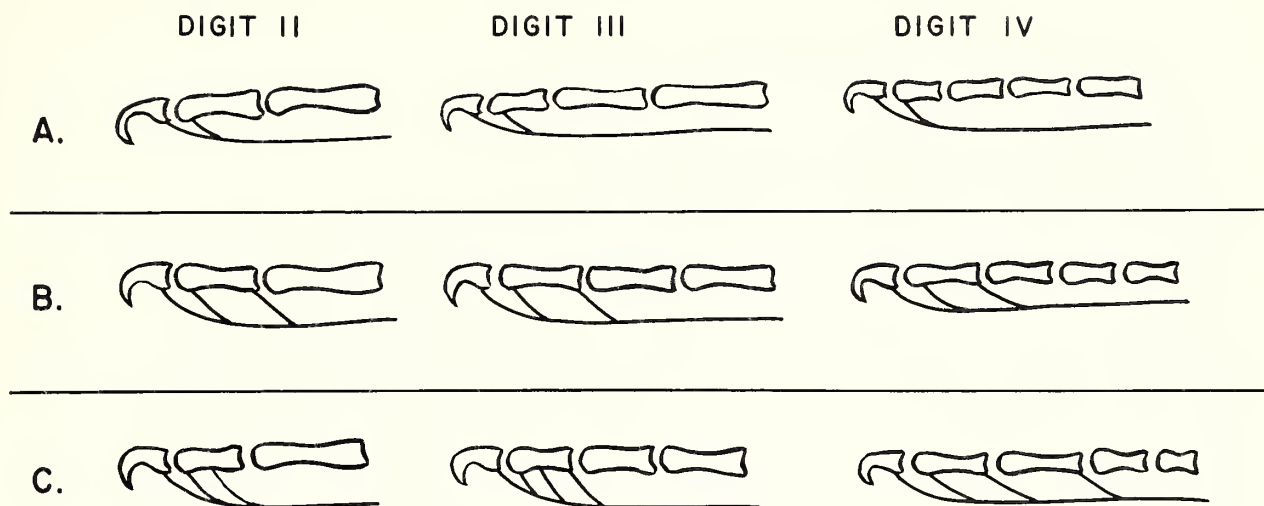


Fig. 8.—Diagram showing the patterns of insertion of the three branches of *M. flexor digitorum longus* on digits II, III, and IV. The formula for insertions can be determined from this diagram. For example, ABB, the most common pattern, means that digit II has the form shown in line A, whereas digits III and IV have the forms shown in line B.

The proximal head shows little variation except that in the vireonid group it is relatively larger compared to the other forms studied. This enlargement is not as striking as the enlargement of *M. flexor hallucis brevis* in the same group, but is perhaps related to it as part of an adaptation for increased strength in movement of the hallux.

M. lumbricalis.—Stallcup (1954) described this muscle in the forms he studied, but Berger (1966, 1968) did not find it in *Agelaius* or *Dendroica*. I found the muscle to be universally present in the

forms studied here. It is small and strap-shaped, and lies deep in the plantar surface of the foot. It arises from the tendon of *M. flexor digitorum longus* just proximal to the point at which that tendon trifurcates, and inserts on the joint pulleys of digits III and IV. No variation was observed. The muscle is very easily stretched, suggesting that in passerines it may be partly or completely converted to an elastic ligament, but this would have to be determined histologically.

CHARACTERIZATION OF TAXA

VIREONIDAE

The genera *Vireo*, *Hylophilus*, *Cyclarhis*, and *Vireolanius* are often included in one family (Mayr and Amadon, 1951; Blake, 1968), but the latter two are sometimes placed in separate families near the Laniidae (Wetmore, 1960). In terms of limb muscles, the four genera are generally primitive in most characters that vary significantly in the New World nine-primaried oscines, but also show some unique derived character states (Tables 3 and 4). The superficial head of *M. gastrocnemius pars interna* is more clearly separate from the deep head than in the other families. The insertion pattern of *M. flexor digitorum longus* is AAB compared to the usual ABB pattern of other families. *M. flexor hallucis*

brevis is greatly enlarged in all four genera; in no other family does it approach this size, and indeed is often so small as to be difficult to identify. These are interpreted as derived states. The tensor propatagialis scapular anchor is absent in the vireonids, but present in the other families. I cannot determine whether this is a derived state, but at least it does separate the vireonids from the other groups. *M. coracobrachialis cranialis* is well developed in *Vireo* and *Vireolanius*, but is reduced in *Hylophilus* and *Cyclarhis*, the latter being a derived state shared with most of the assemblage. This could mean that reduction of the muscle occurred independently in the vireonid radiation and the other families, or that the vireonid genera with reduction are closer to the

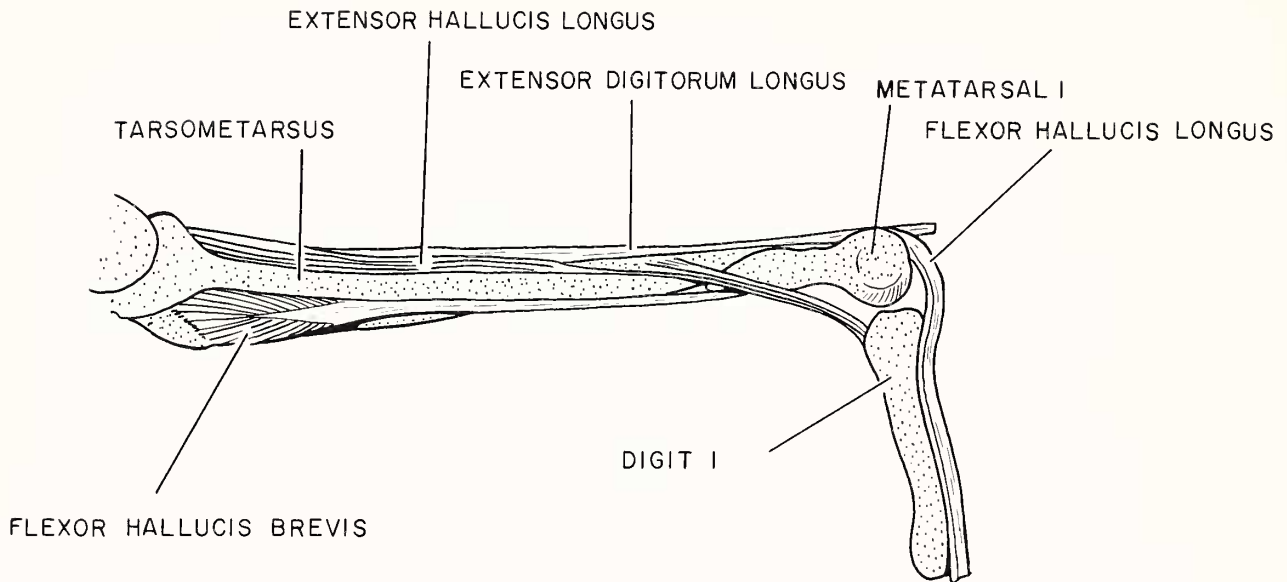


Fig. 9.—Muscles of the tarsometatarsus in *Vireolanus pulchellus*, showing the well-developed flexor hallucis brevis characteristic of the Vireonidae.

origin of the remainder of the assemblage. The *latissimus dorsi pars caudalis* is present in all vireonids, but otherwise almost always absent in the nine-primaried groups.

Are *Cyclarhis* and *Vireolanus* closely related to *Vireo* and *Hylophilus*, and should one family or three be recognized? The derived conditions of *Mm. gastrocnemius pars interna*, *flexor digitorum longus*, *flexor hallucis brevis*, and perhaps *tensor propatagialis* tend to cluster these genera apart from the other families, and indicate that the group as a whole is monophyletic. Retention of *M. latissimus dorsi pars caudalis* supports this, though less strongly as it is a shared primitive character. Furthermore, these genera lack various derived states of several muscles that occur in many nine-primaried families, such as those of *Mm. gastrocnemius*, *obturatorius lateralis*, *plantaris*, and *peroneus brevis*. They are, therefore, clearly related, and a single family is desirable to emphasize both their closeness to each other, and their distinctiveness from the remainder of the assemblage.

A second question concerns the possible relationship of the Vireonidae to the shrikes (Laniidae). Early workers suggested a close relationship, though this is now usually regarded as unlikely, and based mainly on the convergent development of a "toothed" bill. I dissected a typical shrike (*Lanius vittatus*: Laniinae) and a bush shrike (*Telophorus*

dohertyi: Malaconotinae) for comparison. Table 4 shows that the two shrikes are unlike one another, and indeed they represent subfamilies that some workers consider unrelated. This is a separate problem, however. With respect to the vireonids, the main emphasis should be placed on *Lanius* as representative of the "true" shrikes, to which a vireonid relationship is presumably suggested. Table 4 shows little support for this idea. The derived conditions of *Mm. gastrocnemius*, *flexor digitorum longus*, and *flexor hallucis longus* possessed by the vireonids are lacking in the shrikes. The shrikes have a reduced *flexor perforatus digiti III* that is not seen in the vireonids. *Lanius* has a large femoral head of origin on *M. flexor digitorum longus*, which is lacking in the vireonids. The only character shared by the shrikes and vireonids is the retention of *M. latissimus dorsi pars caudalis*, a primitive character state in the passeriformes. In short, the myological evidence fails to support the idea of a close vireonid-laniid relationship.

PARULIDAE

Except for certain genera that appear to be either aberrant or misplaced in this family, and which are discussed separately below, most of the wood warblers examined are myologically similar to each other and generally primitive in their appendicular musculature. They are similar to the Emberizinae,

Table 4.—Myological comparisons of the Vireonidae with other taxa.

Taxa	M. gastrocnemius pars interna, superficial head	M. flexor digitorum longus femoral head	M. flexor digitorum longus insertion	M. flexor perforatus digiti 3	M. flexor hallucis brevis	M. latissimus dorsi caudalis
<i>Vireo</i>	Separate	—	AAB	Normal	Large	+
<i>Hylophilus</i>	Separate	—	AAB	Normal	Large	+
<i>Cyclarhis</i>	Separate	—	AAB	Normal	Large	+
<i>Vireolanius</i>	Separate	—	AAB	Normal	Large	+
<i>Lanius</i>	Partly fused	+	AAA	Reduced	Small	+
<i>Telophorus</i>	Partly fused	—	ABB	Reduced	Medium	+
New World, nine-primaried oscines	Partly fused or lost	—	ABB ¹	Normal	Small	— ²

¹ The few exceptions (Table 3) do not affect the distinction between this group and the Vireonidae.

² Occasionally present (Tables 1 and 2).

although their muscles are often less robust than those of the latter group, which may reflect their more actively arboreal habits and frequently smaller body size. The latissimus dorsi caudalis has been lost, a derived state, whereas the deltoideus minor coracoidal origin is absent, which is a primitive condition in the New World nine-primaried oscine assemblage. M. coracobrachialis cranialis appears to have been entirely lost, as I could not find even a vestige in these forms, though one generally remains in other groups (Table 2). It is possible, however, that some trace of this muscle does remain but was not detected because of the small size of most species. The pronator profundus has the derived condition of two bellies (Type 2) except in *Geothlypis* and *Basileuterus*. This important character state difference suggests that Lowery and Monroe (1968) erred in combining *Oporornis* and *Geothlypis*. M. flexor digitorum profundus, however, is invariably primitive. In the hindlimb the typical parulids are primitive in all the variable muscles described herein, altogether this places the family low on an evolutionary scale within the nine-primaried assemblage.

Seiurus is distinct in several features. In the forelimb of *S. aurocapillus* M. deltoideus minor possesses an origin from the coracoid, which is lacking in typical parulids, as well as in *S. motacilla* and *S. noveboracensis*. In the hindlimb the obturatorius lateralis pars dorsalis is absent (a derived state), except in *S. motacilla*. Most unusual is the presence of a tibial head of M. peroneus brevis. Such a head occurs in other families, but its form here is different. Instead of arising independently from the lat-

eral cnemial crest, it arises from that area in common with the tibial head of M. tibialis cranialis. This indicates that its occurrence here is an independently derived state, and is not homologous with the condition in the cardueline/drepanidid group. It was found in *S. aurocapillus* (two specimens) and *S. motacilla* (one specimen), but not in *S. noveboracensis* (one specimen). The significance of these peculiarities is unknown. Possibly they link *Seiurus* with some unanalyzed oscine family. Alternatively *Seiurus* may indeed be a parulid, whose peculiarities are in some way functionally related to its locomotor habits, as it is much more terrestrial than other parulids. This appears reasonable because *Seiurus* has hybridized with *Dendroica* (Short and Robbins, 1967).

Icteria is larger than other parulids and has been thought not to belong to this family (Ficken and Ficken, 1962; Eisenmann, 1962a; Clark, 1974), but its pelvic muscles are like those of typical parulids. In the forelimb, however, M. deltoideus minor arises in part from the coracoid, a derived condition otherwise found only in some *Seiurus* among the parulids dissected.

Peucedramus is another genus whose placement in the Parulidae has been questioned. George (1962, 1968) suggested that it may be more closely related to the Sylviidae. Its pelvic musculature is like that of typical parulids, but so is that of the Sylviidae examined for the most part (Table 3). In the forelimb M. latissimus dorsi caudalis is retained, which links it more with the Sylviidae than the Parulidae. Likewise, *Peucedramus* has a Type 1 (primitive) pronator profundus as in the Sylviidae, rather than

the Type 2 found in most (but not all) typical parulids. These data are consistent with George's hypothesis of a sylviid relationship.

Zeledonia coronata, the Wrenthrush, was formerly thought to be related to the Turdidae, but Sibley (1968, 1970) studied the egg-white proteins and concluded that it properly belongs among the New World nine-primaried oscines, and probably closest to the Parulidae. Ames (1975) reported that thrushes have a derived condition of the syringeal muscles that is lacking in *Zeledonia*. Hunt (1971) presented life history evidence supporting placement of *Zeledonia* in the New World nine-primaried assemblage. In the thrushes that I examined *M. obturatorius lateralis pars dorsalis* is very large, arising from the entire ventral margin of the ilioischialic fenestra as well as its caudal margin. In *Zeledonia* and the nine-primaried types it arises only from the ventral margin of the fenestra, not the caudal margin. In the general structure of hindlimb muscles *Zeledonia* is typical of the more primitive New World nine-primaried oscines, such as the Parulidae (Table 3). Its large patellar band resembles that of *Basileuterus*, a parulid genus to which relationship of *Zeledonia* has been suggested (Hunt, 1971). In the forelimb *Zeledonia* lacks the latissimus dorsi caudalis as do the parulids. This muscle was present in two of the three turdids examined (Table 2). The flexor digitorum profundus in *Zeledonia* is Type 1 as in the Parulidae, whereas in the Turdidae examined it is Type 2. The most peculiar condition in *Zeledonia* is that the coracobrachialis cranialis is large and stains like a muscle, which is a primitive condition. In both the Parulidae and Turdidae examined this muscle is either reduced to a vestige or lost. Thus, in most respects, the limb myology of *Zeledonia* is similar to that of the Parulidae, but differs from that of the Turdidae.

Compared to the genera of Parulidae dissected, *Zeledonia* is most similar to *Basileuterus*. Both have a maximally developed (1.00) patellar band, which is smaller in the other genera examined except *Wilsonia*. Both also have a Type 1 (primitive) pronator profundus, whereas most other genera (except *Geothlypis*) have a Type 2. (*Peucedramus* also has Type 1, but as discussed above, is probably not a parulid.) These similarities may be significant because Hunt (1971) showed life history similarities of *Zeledonia* and *Basileuterus*, and the two genera also have a similar dorsal coloration and nasal operculum, though these could be convergent (Sibley, 1968). Thus, the results of the present study support

the hypothesis that *Zeledonia* is not a thrush, but is a member of the New World nine-primaried oscines, close to the Parulidae and perhaps especially to *Basileuterus*.

THRAUPIDAE

This family is a classic example of taxonomic confusion resulting from the variety of plumages, sizes, and feeding adaptations that it exhibits (Storer, 1969). The problem is not eased by reducing the group to subfamily status as some have advocated. Not only are relationships within the family difficult, but the affinity of the thraupids to the cardinal finches, parulids, and other groups are also problematical. A number of genera seem to connect the more typical tanagers to one or another of these other groups, and the allocation of these genera forms an additional difficulty. I have dissected only a few of the many tanagers, but even this small sample shows considerable diversity in appendicular muscles. My analysis will not begin to solve the problems surrounding this group, but should contribute to their eventual resolution.

In the forelimb *M. latissimus dorsi caudalis* is generally absent, but was found either bilaterally or unilaterally in some species of *Thraupis* (Tables 1 and 2). The presence of this muscle is inconsistent with the apparent phylogenetic position of the family (see below), and as in the case of its presence in some Icteridae (see discussion under that family) I suspect that its appearance here may be a case of the reestablishment of a previously lost muscle. The coracoidal head of the deltoideus minor (derived) was found only in the aberrant genus *Rhodinocichla*; it was absent in all the more typical tanagers examined. Indeed, in these other forms the scapular portion of the muscle was invariably rather slender compared to its form in other families. The pronator profundus occurs in both primitive and derived states (Table 2).

In the hindlimb (Table 3) both primitive and derived states of the gastrocnemius were found, but otherwise the musculature is generally primitive.

Euphonia and *Tangara* are myologically the most primitive forms studied, with their Type 1 pronator profundus and Type 1 gastrocnemius pars interna. These muscles in the other typical thraupids examined are more highly derived.

Nephelornis oneilli, a new genus and species of nine-primaried oscine, was recently described from Peru (Lowery and Tallman, 1976). *N. oneilli* is a rather nondescript, moderately thin-billed species

Table 5.—Myological comparisons of *Nephelornis* with other taxa.

Muscle	<i>Nephelornis</i>	<i>Urothraupis</i>	Parulidae	Thraupidae	Emberizinae
Gastrocnemius	Type 1	Type 1	Type 1*	Types 1*, 2, 3	Type 1*
Gastrocnemius, patellar band	0.80	0.80	0.50–1.00*	0.50–0.60	0.40–1.00*
Obturatorius lateralis p. dorsalis	Lge.	Lge.	Med. (1 Lge.)	Med., Lge.*	Lge.* (most)
Flexor digitorum longus	ABB	ABA	ABB*	ABB* (most)	ABB*, BBB
Peroneus brevis	±	±	–(1+)	–(few±)*	–
Pronator profundus	1–2	1–2	2* (few 1)	1, 2*	2* (one 1)
Deltoideus minor coracoidal head	–	–	–*(2+)	–*	+(3–)
Deltoideus minor	narrow	narrow	wider	narrow*	wider

* Indicates correspondence with *Nephelornis*.

living in highland cloud forests. Lowery and Tallman (1976) were unable to determine in which family it should be placed. Walter J. Bock examined the jaw and tongue muscles and confirmed that *Nephelornis* is a primitive member of the nine-primaried group (cited in Lowery and Tallman, 1976) but left the question of family position open. The hindlimb myology suggests that *Nephelornis* is closely related to *Urothraupis*, which has been placed in the Thraupidae as recently as 1969 (Storer, 1969), but has been transferred to the Emberizinae by Paynter (1970) without explanation. Relevant comparisons are given in Tables 2, 3, and 5.

The gastrocnemius pars interna is of the primitive type (Type 1) with a relatively wide (0.80) patellar band, in both *Nephelornis* and *Urothraupis*. This falls within the range of variation in Parulidae and Emberizinae. Most Thraupidae have a more derived condition (Type 2 or 3) but *Tangara* and *Euphonia* have the primitive state. *M. obturatorius* lateral pars dorsalis is large in *Nephelornis* and *Urothraupis* as in many thraupids and most emberizines. The insertion pattern of the flexor digitorum longus is ABB in *Nephelornis*, and ABA in *Urothraupis*, which is the only notable difference between the limb muscles of the two genera. ABB is the primitive and usual condition in the New World nine-primaried oscines, and ABA and other variants are rare and show no pattern, so the condition in *Urothraupis* is probably significant only at the generic level.

One possibly significant feature is found in *M. peroneus brevis*. In both *Nephelornis* and *Urothraupis* there is a small band of fibers arising from the ligament to the head of the tibiotarsus. As noted

(Raikow 1977b) this is probably an early stage in the development of a tibial head to the muscle. A rudiment such as this was also seen in *Tangara*, *Coereba*, and *Sericossypha*.

In the forelimb the pronator profundus is intermediate in form between the primitive Type 1 and the derived Type 2, but closer to the latter. The deltoideus minor in both genera lacks a coracoidal head, which is a primitive state, whereas most emberizines possess one, as do a few parulids but no thraupids. Furthermore it is rather slender in these two genera, thus resembling the condition in thraupids. The latter is a rather subjective character, however.

It is apparent that the limb muscles do not provide sufficient information to definitely ally *Nephelornis* with any given family. However, they do show the following points: (1) *Nephelornis* is nearly identical in limb musculature with *Urothraupis*; it is not as similar to any other genus examined. (2) *Nephelornis* (and *Urothraupis*) are clearly very primitive members of the New World nine-primaried assemblage, close to the base of the Thraupidae and Emberizinae. (3) In Table 5 I have marked with an asterisk the families to which each muscle indicates a probable close relationship. There are five similarities to the Parulidae, five to the Emberizinae, and seven to the Thraupidae. The latter include the probably significant similarities in the peroneus brevis and deltoideus minor. (4) The other families in the assemblage are more highly derived in various characters and are, therefore, of no concern to this problem.

The bill of *Nephelornis* is rather slender, and the jaws show little deflection, which suggests little if

any adaptation for seed-eating. Lowery and Tallman (1976) reported that it fed mainly on insects, and found no seeds in stomachs examined. This suggests that it is more primitive in feeding habits than typical emberizines, though it is clear that more investigation of both its feeding habits and feeding mechanism are needed.

There is thus a conflict of evidence concerning familial position. The limb myology favors inclusion of *Nephelornis* and *Urothraupis* in the Thraupidae. This family is traditionally regarded as being characterized by fruit-eating in addition to insectivory. I have no information on the food of *Urothraupis* and the few data on *Nephelornis* suggest a concentration on insects, along with a small amount of plant material.

On the basis of the foregoing discussion I conclude that *Nephelornis* is a very primitive member of the New World nine-primaried oscine assemblage, and that it is little modified from the primitive basal stock from which the early Thraupidae and Emberizinae arose. *Nephelornis* is thus of interest because it more closely approaches this hypothetical ancestor than any other genus examined, except *Urothraupis*. On the basis of limb musculature alone, I would hesitate to separate the genera. I suggest on the basis of present knowledge that for the purpose of classification *Nephelornis* be considered a very primitive member of the Thraupidae, and that *Urothraupis* be returned to this family, adjacent to *Nephelornis*.

Rhodinocichla has been placed in various families but no solution has been entirely satisfactory. Skutch (1962) argued on the basis of behavior that its affinities lie with the Mimidae, whereas Eisenmann (1962b) concluded mainly from morphology that it is a tanager; this was supported by Clark (1974). A study of the limb myology only confuses the picture more. The latissimus dorsi caudalis is absent as in most tanagers, whereas in *Dumetella* it is present. The deltoideus minor has a coracoidal head, unlike either *Dumetella* or thraupids. The pronator profundus in *Rhodinocichla* is the Type 1, whereas in *Dumetella* it is Type 2. Both types occur among Thraupidae, but Type 1 was found only in a few forms. These data tend to support the thraupid theory rather than the mimid theory, but the limited evidence is hardly convincing. The problem is complicated because *Rhodinocichla* has several unique myological conditions that are not found in either the Mimidae or Thraupidae. The flexor digi-

torum longus has a CBB insertion pattern (Fig. 8), which I found in no other form examined. The extensor secundariorum inserts only on two secondaries, rather than the usual three. The flexor perforatus digiti II has a secondary head as described above, which is not found in any other form dissected. The limb myology, then, shows *Rhodinocichla* to be even more distinctive than previously supposed, but does not help in determining in which family it should be placed. For the present it is most practical to retain *Rhodinocichla* in the Thraupidae until other evidence suggests an alternative.

Sericossypha is the most myologically aberrant tanager dissected, with its centrally reduced iliotibialis lateralis, and well-developed femoral head of M. flexor digitorum longus, both unique conditions in the New World nine-primaried oscines studied. It also has a partial tibial head to M. peroneus brevis, and unusually large Mm. flexor hallucis brevis and extensor hallucis longus. This pattern of peculiar features does not resemble any other form studied, and so its relationships remain obscure.

Catamblyrhynchus is a distinctive genus of uncertain affinities, sometimes being placed in the Thraupidae and sometimes in a family Catamblyrhynchidae. The interosseus dorsalis is vestigial, an autapomorphic character that does not assist in determining the relationships of the genus. The coracobrachialis cranialis is well developed, a primitive condition. The deltoideus minor, which lacks a coracoidal head, is slender as in the Thraupidae.

The pelvic musculature is primitive with respect to Mm. gastrocnemius, obturator lateralis, and peroneus brevis. The ABA insertion pattern of the flexor digitorum longus does not occur in thraupids, but was found in several other families as a variant, and probably has no significance. The absence of the plantaris is a derived state. Altogether, the limb myology places *Catamblyrhynchus* within the nine-primaried assemblage as a relatively primitive, but in some ways distinct form, lying close to the parulid/emberizine/thraupid group. The robustness and length of the shank muscles, however, set it apart from the Parulidae. The bill, although superficially finchlike, differs in detail from that of true finches. The tip of the bill is abruptly squared off when seen from above, and there are peculiar grooves running forward from the nostril on either side. Furthermore there is hardly any indication of an angled commissure, as is typical of finches. All this suggests that the resemblance of the bill is a superficial

case of convergence, and does not indicate that *Catamblyrhynchus* is a modified emberizine, as suggested by Paynter (1970).

On the basis of these observations my inclination is to regard *Catamblyrhynchus* as most probably an early offshoot of the Thraupidae, and to regard it taxonomically as rather distinct within that family. I do not advocate giving it full family status as that obscures its probable affinity with the Thraupidae.

The Swallow Tanager, *Tersina viridis*, is unusual because of its flycatching behavior. It is sometimes included in the Thraupidae, and sometimes placed in a monotypic family Tersinidae. *Tersina* was found to have a few unusual myological characteristics. *M. serratus superficialis pars costohumeralis* arises from the fourth true rib, rather than the third as in most species studied. *M. flexor digitorum profundus* narrows distally rather than in Icteridae (Type 2), though the similarity must certainly be convergent. *M. extensor digitorum communis* has an elongated belly. The *flexor digitorum longus* has an ACB insertion pattern, rather than the usual ABB. Otherwise the myological conditions fall within the usual range of variation in the Thraupidae (Tables 2 and 3). The several distinctive conditions in the forelimb could possibly represent modifications somehow related to flycatching.

COEREBIDAE

This family was long maintained for a group of nectar-feeding genera though it was recognized that some were close to the Parulidae and some to the Thraupidae. Following Beecher (1951a) *Coereba* and *Conirostrum* (including *Ateleodacnis*) are now generally placed in the Parulidae, and *Cyanerpes*, *Diglossa*, *Dacnis*, *Chlorophanes*, *Euneornis*, *Hemidacnis*, *Iridophanes*, *Xenodacnis*, and *Oreomanes* in the Thraupidae. It is generally believed that nectar feeding arose at least twice and perhaps several times independently in this assemblage. I have dissected the first seven of the above 11 genera. There are some variations, but no derived specializations that would cluster the genera into a separate family. *Coereba* and *Conirostrum* fit easily into the range of variation in the Parulidae, being more like typical wood warblers than are such aberrant forms as *Seiurus* and even *Icteria*. The only peculiarity is a small partial tibial head of the *peroneus brevis* in *Coereba*, a feature that occurs in some members of several other groups.

The Thraupidae have more limb muscle variation

than do the Parulidae, but again the related "coerebid" genera fit easily among them. All have the derived state of the *pronator profundus*, while both primitive and derived forms occur among the Thraupidae. *Dacnis*, *Diglossa*, *Chlorophanes*, and *Euneornis* retain the patellar band of the *gastrocnemius*, whereas in *Cyanerpes* and several typical tanagers it is lost. The essential coherence of this group is further attested by the successful hybridization of such diverse genera as *Cyanerpes* and *Tangara* (Delacour, 1972).

EMBERIZINAE

The emberizine finches show great uniformity in their appendicular musculature. They are similar to the Parulidae except that their muscles tend to be heavier and the shank muscles tend to extend farther along the length of the tibiotarsus than in the wood warblers. In the forelimb the *latissimus dorsi caudalis* is absent, *M. coracobrachialis cranialis* is vestigial or lost, and with one exception the *pronator profundus* is of the derived type. The emberizines agree with the parulids in these derived states, and also share the primitive condition of *M. flexor digitorum profundus*. However, unlike typical parulids the *deltoideus minor* has in most cases an expanded area of origin from the coracoid, a derived state.

In the hindlimb all forms studied have the primitive state in *Mm. gastrocnemius*, *obturatorius lateralis*, *plantaris*, and *peroneus brevis*. The patellar band and the dorsal head of *M. obturatorius lateralis* are both large, showing no trends toward reduction. However, the emberizine finches are generally primitive and show little variation in their appendicular muscles.

CARDINALINAE

The cardinal finches show a small amount of myological diversity in both limbs. The *deltoideus minor* coracoidal head may be present or absent. *Saltator* has a well-developed *coracobrachialis cranialis*, a muscle that is reduced to a vestige in most forms studied. In the hindlimb the *gastrocnemius pars interna* varies from the most primitive to the most derived conditions. As a whole, this group cannot be distinctly separated from either the emberizine finches or the tanagers on the basis of limb myology.

ICTERIDAE

The Icteridae are of particular interest because the family has undergone a considerable adaptive radiation in feeding specializations and related behavior (Beecher, 1951*b*; Lowther, 1975). It includes both terrestrial and arboreal types ranging from smaller, short-billed genera like *Spiza*, *Dolichonyx*, and *Molothrus* that closely resemble emberizine finches, to large long-billed arboreal foragers like *Cacicus* and *Psarocolius*.

In the forelimb the Icteridae show a modification of the flexor digitorum profundus in which the caudal border of the muscle is narrowed (Fig. 4). Though this is not a profound modification, it is found without exception in all forms examined, and this consistency suggests that it is a reliable character useful in defining the family. The pronator profundus and deltoideus minor show the derived state in most forms, but are primitive in a few.

The occurrence of *M. latissimus dorsi pars caudalis* in a few icterids is especially intriguing (Table 1). This muscle occurs consistently only in the Virconidae (Table 2). Its presence in a few members of an otherwise advanced group is difficult to explain. Possibly the muscle was retained in the history of the group, and was lost independently in many lineages, including most of the icterids, but I believe it possible that its presence here may be an example of a reestablished condition. In other words, the muscle (or rather its expression in the phenotype) may have been lost early in the evolution of the nine-primaried assemblage, but the genetic information for its production could have been retained and later reactivated in a few forms. This is suggested by the distribution of the muscle in the Icteridae (Table 2). It occurs in some species of a genus, and not in others; it may even occur on one side of the body only in some specimens. This suggests an easily perturbed genetic mechanism controlling its appearance. A similar phenomenon was also found in some Thraupidae. The reappearance of "lost" ancestral muscles in birds is discussed elsewhere (Raikow, 1975; Raikow and Borecky, in preparation).

The muscles of the hindlimb are similar to those of the emberizines except that the patellar band of the gastrocnemius pars interna is always absent (Type 2 or 3), a derived condition whereas in the emberizines it is Type 1.

Spiza requires special mention because of its controversial taxonomic status. Sibley (1970) and Tordoff (1954) placed it among the cardinaline (rich-

mondennine) finches, whereas Sushkin (1925) considered it intermediate between the Emberizinae and Icteridae and arbitrarily placed it in the former group for convenience. Beecher (1951*b*) considered it an icterid on the basis of jaw muscles and the horny palate. The forelimb myology tends to support the icterid theory. *Spiza* has a Type 2 flexor digitorum profundus as in the Icteridae, whereas the Cardinalinae have a Type 1 muscle.

In *Sturnella* the forelimb is typically icterid, but the hindlimb is distinctive in several ways. The dorsal head of the obturatorius lateralis is absent, unlike all other genera studied, where it is relatively large. The aponeurosis of origin of *M. adductor femoris pars caudalis* is very short. The superficial head of *M. gastrocnemius pars interna* is very well developed and separate for most of its length from the deep head. The tendon of *M. flexor perforans et perforatus digiti III* is ossified in the shank and tarsus, and the tendon of *M. peroneus longus* is ossified from the belly to its bifurcation near the tibial cartilage. The lateral head of *M. flexor hallucis longus* arises about 3 mm proximal to the iliofibularis insertion, whereas in other forms it arises just distal to this insertion. The intermediate and medial heads of *M. flexor hallucis longus* are not clearly separable. The significance of these variations is unknown, but perhaps they are functionally related to the terrestrial habits of this form. In this regard it may be significant that in *Dolichonyx*, another terrestrial genus, the gastrocnemius pars interna has a form similar to that in *Sturnella*.

CARDUELINAE

The cardueline finches show little variation in the forelimb musculature but a great deal in the hindlimb. The only variation found in the forelimb is in *M. deltoideus minor*—most forms possess a coracoidal head (derived state) but it is lacking in *Fringilla* and in *Carpodacus cassini* and *C. purpureus* (but was present in *C. mexicanus*). This suggests that its absence in the latter genus, which on the basis of its pelvic myology is a fairly advanced member of the family, is probably due to secondary loss in some species. Its absence in *Fringilla*, however, is probably primitive, as is discussed below.

There is considerable diversity in the hindlimb muscles (Table 3). *M. gastrocnemius pars interna* shows a complete range of structure from the most primitive through the most derived conditions. The dorsal head of *M. obturatorius lateralis* is present in some forms, and absent in others. When present,

however, it is of medium or (usually) small size, showing a general trend throughout the family for reduction and loss of the muscle. The tibial head of *M. peroneus brevis* may be absent, partially developed, or completely developed. *M. plantaris* may be present or absent. Furthermore, the diversity is increased by the several combinations of variations found in different species. This diversity characterizes the *Carduelinae* as a progressive and rapidly evolving group.

There are several taxonomic problems involving the *Carduelinae* to which the present study can contribute useful insights. First, are the carduelines more closely allied with the Old World finches (*Ploceidae* and *Estrildidae*) or the New World finches (*Emberizinae* and *Cardinalinae*)? Tordoff (1954) argued on the basis of palatal osteology that the group is unrelated to the latter and placed it as a subfamily of the *Ploceidae*, but few workers have supported this. Bentz (1976) described the limb myology of the *Ploceidae* and *Estrildidae* and some of his findings are briefly summarized in Tables 2 and 3. Many of the Old World forms retain the *laticostimus dorsalis pars caudalis*, which is totally absent in the carduelines. Bentz did not find the tensor *propatagialis scapularis* tendon in his study, whereas it is always present in the *Carduelinae*. The *deltoideus minor* lacks a coracoidal head in most *Ploceidae*/*Estrildidae*, but is almost universally present in the *Carduelinae*. The *pronator profundus* is Type 1 in all ploceids and most estrildids, but is Type 2 in all carduelines. The *peroneus brevis* has a tibial head in many carduelines, but never in the *Ploceidae* or *Estrildidae*. Altogether, the limb myology supports the theory that the *Carduelinae* are part of the New World nine-primaried oscine assemblage and are not closely related to the ploceid/estrildid complex.

A second problem is the relationship of the *Carduelinae* to the genus *Fringilla*. Sibley (1970:100–103) reviewed this problem in detail. Bock (1960:476) suggested that *Fringilla* is intermediate between the *Emberizinae* and the *Carduelinae*, and the limb muscle data are consistent with this view. The *deltoideus minor* lacks a coracoidal head in *Fringilla*, a primitive state found in a few emberizines (Table 2), but only in some species of one of the cardueline genera studied. The *gastrocnemius pars interna* shows a derived state in *Fringilla*, like most carduelines rather than emberizines, but in other respects its limb myology is generally primitive. In terms of pelvic muscle structure *Leucostic-*

te is even more primitive than *Fringilla*, as it is the only cardueline retaining the Type 1 *gastrocnemius pars interna*. *Leucosticte* also has a relatively primitive tongue structure, more like that of some emberizines than that of the more advanced carduelines (Raikow, 1977b). Tordoff (1954) showed that in the carduelines the head of the humerus is relatively broader than in the emberizines, but that this trait was least developed in *Leucosticte*. These considerations suggest that *Leucosticte* rather than *Fringilla* might be better regarded as the most primitive of the cardueline genera investigated.

Finally, there has been much discussion of the relationship of the *Carduelinae* and the *Drepanididae*. The drepanidid genus *Psittirostra* is anatomically essentially a cardueline, and the two families appear to be sister groups. This is discussed further below.

DREPANIDIDAE

The history of drepanidid classification was reviewed by Sibley (1970:104). Early workers placed the different genera in several families, allying the finchlike *Psittirostra* with the *Fringillidae*, and the nectar-feeding forms with Old World nectar-feeders (*Dicaeidae* and *Meliphagidae*). Later they were recognized as constituting a single assemblage despite their diversity. Some workers were impressed by the nectar-feeding adaptations of many *Drepanidids* and supposed their ancestors to be either the *Coelebatidae* or *Thraupidae*. Others have been more impressed by similarities between the finch-billed *Drepanididae* and the cardueline finches. Beecher (1953) found similarities in the jaw muscles between the groups. Sushkin (1929) allied the *Drepanididae* and *Carduelinae* on the basis of the bill, skull, and horny palate. Bock (1960) suggested that the *Carduelinae* lack specialized features that would preclude their ancestry of the *Drepanididae*, and that they have a tendency to wander erratically in flocks, a habit that might be expected in a colonizing group.

The pelvic musculature of the *Drepanididae* is relatively uniform (Table 3), including both subfamilies. This reinforces the idea that the family is derived from a single founding species. The *M. gastrocnemius pars interna* in all forms studied is Type 1, the most primitive sort. Among the *Carduelinae* only *Leucosticte* shows this condition; all other genera examined have derived conditions 2 or 3 for this character. The dorsal head of *M. obturatorius lateralis* is present in all forms; again this is the

ancestral state, whereas both conditions occur among carduelines. The plantaris muscle is present (primitive state) in most Drepanididae, but absent (derived state) in three species; the Carduelinae also include both conditions. Of greatest significance is the *M. peroneus brevis*. In all Drepanididae examined this muscle has a fully developed tibial head. As noted above, this is a derived character state of infrequent occurrence. The only other New World, nine-primaried group that regularly shows this character state is the Carduelinae, where it occurs in a majority of genera. These observations suggest strongly that the Carduelinae are the closest relatives of the Drepanididae.

The carduelines have evolved considerably since the time that they split off from the ancestral Drepanididae. The derived state of *M. gastrocnemius pars interna* must have arisen after this separation.

The ancestral state was retained in the Drepanididae, but only the genus *Leucosticte* among the forms studied still shows it in the Carduelinae; other genera have progressed to more derived states. Partly on the basis of the evidence cited above I feel that the Drepanididae are best regarded as an offshoot of a fairly primitive cardueline species, though one in which the tibial head of *M. peroneus brevis* had already developed. They have remained relatively conservative in their pelvic myology while radiating spectacularly in their feeding apparatus. The Carduelinae in contrast have radiated more in their pelvic musculature since the separation of the two lineages, but less so in their feeding apparatus. A more detailed analysis of the drepanidid-cardueline relationship is presented elsewhere (Raikow 1977b).

A PHYLOGENY OF THE NEW WORLD NINE-PRIMARIED OSCINES

I will now present a phylogeny of the New World nine-primaried oscines as a hypothesis of the pattern of ancestral relationships in the group to the degree that present information makes possible. This model phylogeny is based on the idea that the major groups are the products of adaptive radiations into discrete adaptive zones defined mainly in terms of feeding specializations, and involving the structure of the feeding apparatus, the methods of foraging, and the types of foods taken. Many writers have suggested that feeding specializations are "adaptive" and hence poor indicators of relationships because of the supposed ease with which divergent groups may come to resemble each other through convergence. Thus "bill shape," formerly an important taxonomic character, is now in disrepute. These criticisms are valid only insofar as comparison is superficial and limited to simple structures, but, if a whole adaptive complex is examined in some detail, it should be possible to recognize convergence in most cases. This can be tested by comparing the feeding system with information from other sources, such as the limb muscles studied herein. The present classification of the New World nine-primaried oscines is to a great extent based on feeding adaptations, so the present analysis is an attempt to see whether this concept is a valid model for a theory of phylogenetic relationships within the group.

This type of evolutionary pattern has been discussed by various workers including Schaefer (1976), Mayr (1976), and Bock (1965). Basically, it is suggested that an evolving lineage may enter a new adaptive zone by developing a new structural and behavioral specialization that allows it to exploit the environment in a manner not highly competitive with other organisms. This could involve the use of a new kind of food, or the ability to feed in places formerly unreachable. When this happens, the way is open for an extensive radiation of the pioneering group into a variety of specialized sub-zones of the general adaptive zone. For example, once a mechanism was developed for cracking hard-shelled seeds, specializations could occur in the relative size of the bill, in bill shape, in the mechanics of jaw action, in the structure of the tongue, and in the locomotor apparatus, making possible a radiation into specific feeding niches defined by the size and hardness of the seeds taken, the substrate on which foraging occurs, and so forth.

Fig. 10 is a cladogram representing the phylogeny of the New World nine-primaried oscines analyzed at the generic level for most of the forms dissected in the present study. Especially uncertain relationships are indicated as dotted lines; some of these show alternative possibilities. This phylogeny is not intended as a final solution to the problem of relationships among the birds studied; rather it is a hy-

pothesis representing what I consider to be the most reasonable interpretation of the information available at the present time. It is presented as a framework for discussion of the possible history of the New World nine-primaried oscines and to point out specific problem areas where further research is particularly needed.

We must first deal with the problem of the Vireonidae. Sibley (1970:170) reviewed the taxonomic history of this family; the general opinion today is that the family Vireonidae is related to the New World nine-primaried oscines, but is somewhat set apart from the other families. The remainder of the group is clustered by a collection of synapomorphies and corroborating noncladistic data that exclude the Vireonidae. Both in the characteristics reviewed earlier, and in the limb muscle structure reported herein, the Vireonidae do not appear to be part of this otherwise monophyletic group. They share none of the evolutionary trends in limb muscle structure seen in the other families. In addition, they have several derived states not found in the other families, including the separation of the superficial head of *M. gastrocnemius pars interna*, the enlargement of *flexor hallucis brevis*, and the *flexor digitorum longus* insertion. Furthermore they lack the *tensor propatagialis scapular* anchor and retain the *latissimus dorsi caudalis*. Except for Beecher's (1953) belief that the jaw muscles show an ancestral relationship to the Parulidae, there is no compelling evidence, and most importantly, no shared derived character states that group the Vireonidae with the other New World nine-primaried oscines. Therefore, it must be concluded that the Vireonidae have at most only a distant phylogenetic link to this group, and should not be included within it.

CLUSTER 1

With the exclusion of the Vireonidae, the remainder of the New World nine-primaried assemblage clearly appears monophyletic on the basis of apparent synapomorphies (reduced tenth primary, pneumatic fossa of humerus, compressed basihyale with attached *hyoglossus obliquus*, and loss of *latissimus dorsi caudalis*) supported by noncladistic evidences (egg-white proteins, pterylosis, and pattern of adaptive diversity) as discussed in detail above.

The Parulidae are in general the most primitive group of this assemblage on the basis of their limb muscles, although a few genera depart from the typical condition of the family in certain muscles. This

general condition is correlated with the widely held idea that purely insectivorous habits are more primitive than feeding on plants. *Dendroica*, *Mniotilta*, *Oporornis*, *Myioborus*, and *Wilsonia* are "typical" wood warblers showing the derived state of *M. pronator profundus* (1a), but not separable from each other by any characters analyzed herein. *Geothlypis* and *Basileuterus* are similar except for possession (presumably retention) of the primitive state of *M. pronator profundus*. *Zeledonia* is very primitive myologically, even to the retention of a well-developed *M. coracobrachialis cranialis*. It is placed beside *Basileuterus*, with which it possibly has a relatively recent common ancestor as discussed above. The reduction of its flight mechanism is autapomorphous (1b).

The "coerebid-parulids" *Coereba* and *Coniosturum* are essentially typical parulids in their limb muscles. They are clustered here (1c) because they share nectar-feeding adaptations. It is uncertain whether this is really a synapomorphy; quite possibly they evolved this specialization independently and do not share a nectar-feeding common ancestor. Limb myology cannot resolve this problem, but a study of the feeding apparatus might possibly do so.

Seiurus and *Icteria* are clustered by the common possession of a coracoidal origin of *M. deltoideus minor* (1d). However, each is so distinctive (1e, 1f, and discussion above) that I consider it doubtful that they are closely related; more likely they evolved this derived state independently, especially because it only occurs in one of the three genera of *Seiurus* examined. Their placement here is very speculative, and mainly serves to point out the need for additional studies of their relationships.

Nephelornis and *Urothraupis* are morphologically similar to each other, but their exact position remains uncertain pending further studies. However, they are myologically primitive and must lie somewhere close to the position shown, near the border of the Parulidae and Thraupidae.

CLUSTER 2

The Parulidae are almost entirely insectivorous, whereas the emberizine, cardinaline, and cardueline finches eat seeds as well, as do the more primitive members of the highly diversified Icteridae and Drepanididae. This provides a spectrum of feeding specializations in the New World nine-primaried assemblage; the problem has been to determine which is the primitive end of the spectrum (for ex-

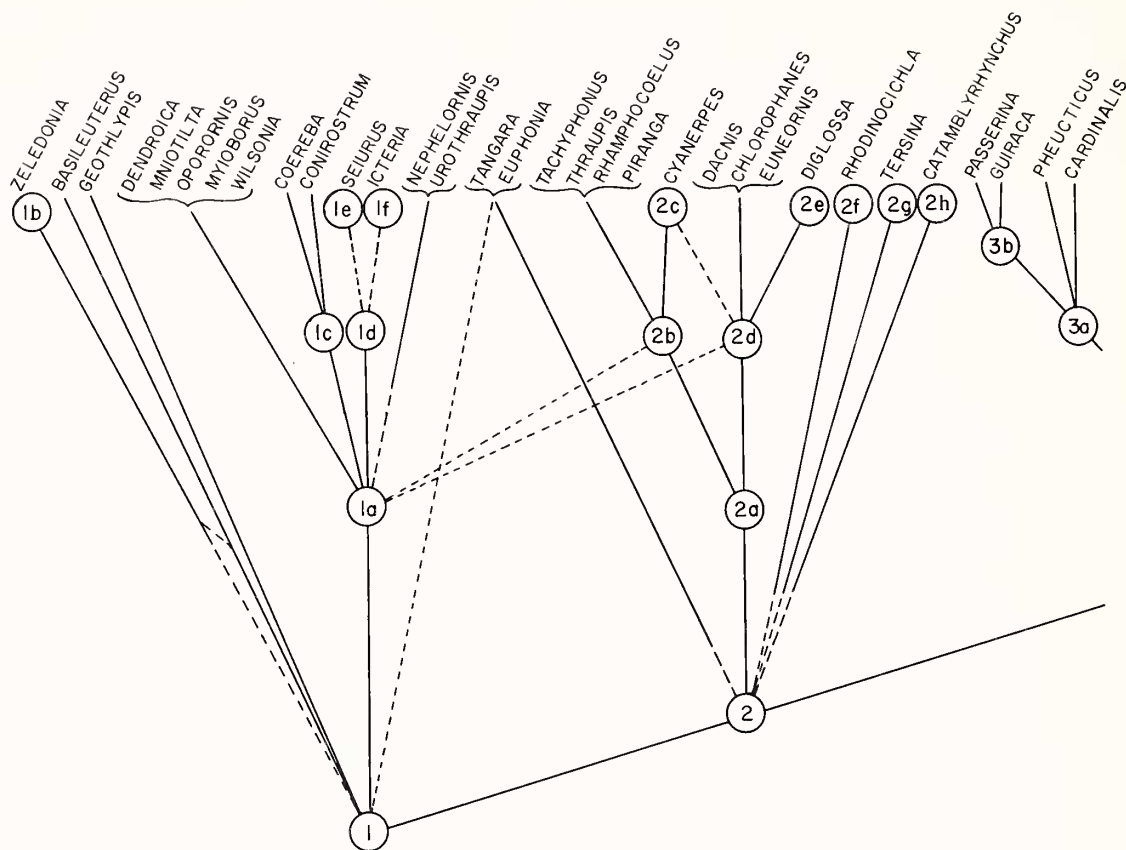


Fig. 10A.—A cladogram suggesting phylogenetic relationships in the New World nine-primaried oscines. Numbers in circles designate presumed shared derived character states. See text for discussion. 1. Reduced tenth primary; fully developed pneumatic fossa; compressed basihyale with attached hyoglossus obliquus; latissimus dorsi caudalis lost. Supportive noncladistic data: egg-white protein similarities; indistinct family boundaries; pattern of adaptive diversity; pterylography. 1a. Type 2 pronator profundus. 1b. Reduction of wings and near loss of flight. 1c. Nectar feeding. 1d. Deltoideus minor coracoidal head added. 1e. Peroneus brevis tibial head added; obturatorius lateralis dorsalis lost. 1f. Large size; deltoideus minor coracoidal origin. 2. Feeding on fruits added to insectivory; bill heavier but lacking pronounced deflection. 2a. Type 2 pronator profundus. 2b. Patellar band of gastrocnemius lost. 2c. Plantaris lost; nectar feeding. 2d. Nectar feeding. 2e. Plantaris lost. 2f. Flexor digitorum longus type CBB; deltoideus minor coracoidal head added; flexor perforatus digiti 2 extra head added. 2g. Serratus superficialis from 4th rib; flexor digitorum profundus type 2; flexor digitorum longus ACB; wide bill and flycatching. 2h. Interosseus dorsalis vestigial; coracobrachialis cranialis well developed; flexor digitorum longus ABA; plantaris lost. 3. Bill shorter and deeper, with pronounced deflection; seeds eaten, nutcracker method; deltoideus minor coracoidal head added. 3a. Bill still heavier; feed on larger percentage of seeds and often larger seeds, fewer insects. 3b. Patellar band of gastrocnemius lost.

ample, Mayr, 1955:34). The limb muscle data analyzed herein provide a solution to this problem; as most workers have suspected at least intuitively, the seed-eating habit is a derived specialization as shown by its correlation with limb muscle evolution. However, seed-eating is a highly specialized condition requiring extreme structural modifications of the feeding apparatus, and it is unlikely that it evolved suddenly in insectivorous forms. More likely birds first began eating the softer tissues of

fruits, and gradually moved up to the harder seeds. Fruit-eating is a likely intermediate stage in the evolution of herbivorous habits, and thus the Thraupidae appear to represent a probably intermediate stage between purely insectivorous types (Parulidae) and the advanced granivores. The Thraupidae are a diverse group, some members being quite thin-billed and difficult to separate from the Parulidae, others being more intermediate, and still others closely approaching the cardinaline and ember-

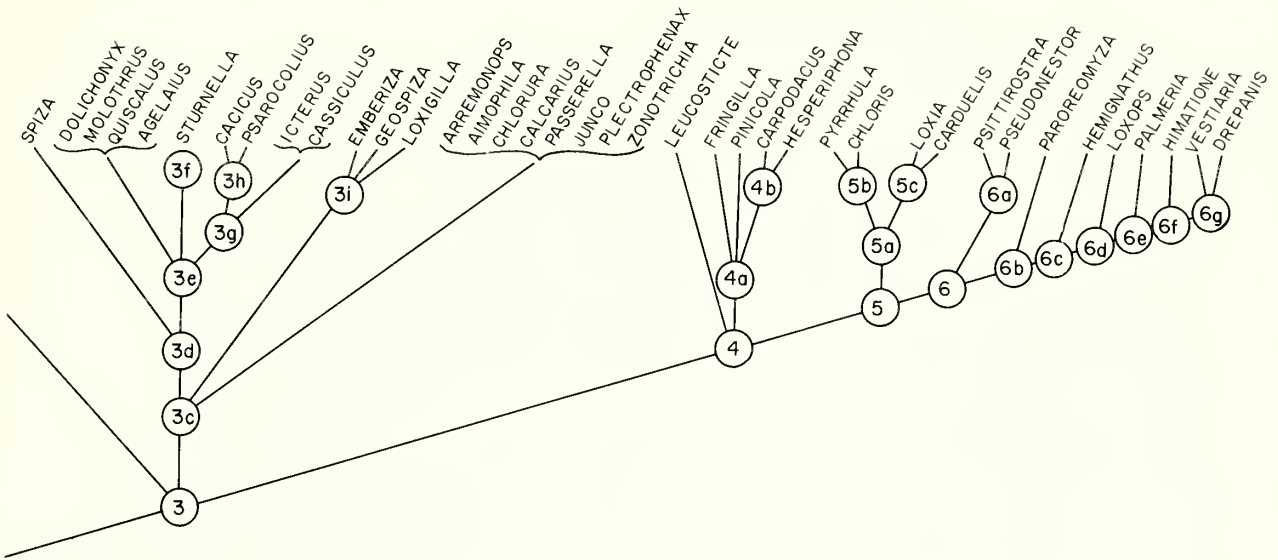


Fig. 10B.—3c. Ground-foraging habits, sometimes with double-scratch method. 3d. Patellar band of gastrocnemius lost; flexor digitorum profundus Type 2. 3e. Rictal bristles reduced or lost. 3f. Obturatorius lateralis dorsalis lost. 3g. Primarily arboreal habits. 3h. Pronator profundus Type 1. 3i. Deltoideus minor coracoidal origin lost. 4. Bill heavier, with vise method of seed cracking; obturatorius lateralis dorsalis reduced. 4a. Patellar band of gastrocnemius lost. 4b. Plantaris lost. 5. Peroneus brevis tibial head added. 5a. Patellar band lost. 5b. Obturatorius lateralis dorsalis lost. 5c. Plantaris lost. 6. Colonization of Hawaiian Islands. Supportive noncladistic data: near uniformity of limb muscles throughout family. 6a. Bill enlarged with increased overlap of upper mandible. 6b. Bill, tongue, and nares elongated. 6c. Tubular tongue; enlargement of nasal operculum with convex margin. 6d. Plantaris lost. 6e. Nasal operculum larger and more flattened; plumage harder and less fluffy. 6f. Nasal operculum still larger, anterior notch added; primaries truncate. 6g. Bill elongated and decurved.

izine finches. Thus the family seems to contain genera representing various stages in the evolution of the seed-eating types. In their limb myology the thraupids are generally rather primitive, but various genera differ in the possession of several derived conditions. More than any other family, this one is difficult to characterize as monophyletic, because the Thraupidae are not clustered by any important synapomorphies. The best solution, which I recognize as very imperfect, is to regard the Thraupidae as probably representing more a structural/behavioral grade than a monophyletic taxon, and to place it in this position as being more highly derived than the Parulidae but more primitive than those families with clear specializations for seed cracking. The following discussion and conclusions are rather tentative because I have studied only a small extent of the range of diversity that occurs in the Thraupidae. Many more genera must be examined in order to clarify the problems in this group.

Point (2) indicates the development of herbivorous habits and in correlation, a heavier bill. The forms radiating from point (2) constitute the hetero-

ogeneous thraupid assemblage, plus the ancestral lineage of the seedeaters. *Tangara* and *Euphonia* are the most primitive genera in limb myology; their Type 1 pronator profundus is more primitive than even the typical parulid condition. If we assume that the evolution of herbivory in addition to insectivory occurred only once, so that the thraupid assemblage is monophyletic in the strictest sense, then these genera will arise as shown from point (2) in Fig. 10. This assumption is certainly parsimonious, but is also very simplistic and probably false. On the basis of their primitive limb myology these two genera could also have arisen earlier within the primitive insectivorous ancestry of the assemblage, as shown by the alternative pathway leading from point (1). In this case they would have developed herbivorous adaptations independently of other Thraupidae. Here is a case where a study of the feeding mechanism could prove helpful.

Tachyphonus, *Thraupis*, *Rhamphococelus*, and *Piranga* are "typical" tanagers and essentially alike in limb myology. They share synapomorphous states of *M. pronator profundus* (2a) and *M. gas-*

trocnemius (2b). *Cyanerpes* has these features plus the loss of *M. plantaris* and the addition of nectar feeding (2c). Again, this group is part of the radiation of a monophyletic Thraupidae if we hold to the assumption of a single origin of herbivory. However, if we do not insist on this, then the genera arising from (2b) could, on the basis of limb myology, also have arisen from point (1a) instead, as shown by the dotted line in Fig. 10.

The "coerebid-thraupids" *Dacnis*, *Chlorophanes*, and *Ennerornis* are similar in limb myology; *Diglossa* has an additional derived state in the loss of *M. plantaris* (2e). These forms are clustered on the basis of a presumed common origin of nectar-feeding adaptations (2d). As with *Coereba* and *Conirostrum* in the Parulidae, this is an expedient, parsimonious, and tentative placement pending future analysis of the feeding mechanism. Again, these forms could arise via (1a) rather than (2a) if the assumption of monophyletic herbivory is not held to, as shown in Fig. 10. If *Cyanerpes* is also hypothesized as part of a single radiation of nectar-feeding forms, then its loss of the patellar band (2b) must have occurred independently.

As discussed earlier, *Rhodinocichla*, *Tersina*, and *Catamblyrhynchus* lie within the thraupid assemblage, but on the basis of limb myology these traditionally problematic forms remain troublesome (2f, 2g, 2h).

The depiction of the thraupid radiation arising from a single point (2) implying a single common ancestor for the group is undoubtedly a gross oversimplification. It appears intuitively likely that several lineages independently developed herbivorous feeding adaptations, as suggested by the alternative phylogenies shown in Fig. 10. Only a few thraupid genera were dissected in this study, and the true phylogeny of the group must be far more complex than that shown here. The limited analysis of limb myology has not solved this problem, but it has clearly shown that the analysis of the limb muscles can support a hypothesis of a polyphyletic family Thraupidae.

CLUSTER 3

These groups are clustered by a feeding apparatus adapted for cracking seeds. Exceptions are some icterids and drepanidids with feeding mechanisms otherwise specialized, but which are clearly derived within their families, the more primitive members of which possess the seed-eating adaptations. This adaptation is presumably derived by fur-

ther specialization from the principally fruit-eating Thraupidae. Bock (1960) analyzed the functional anatomy of the feeding mechanism. The emberizines show a relatively modest development of this system, and feed on relatively smaller seeds, using a biomechanical system that Bock termed the "nut-cracker" method. Cardinalines use the same method, but have larger bills and eat larger seeds.

This group is also clustered by possession of a derived character state in a wing muscle, the presence of a coracoidal head to *M. deltoideus minor*. There are a few exceptions, however. A few genera of most of these families have the primitive state, and a few parulids and one (presumed) thraupid have the derived state (Table 2). Nevertheless, nearly all parulids and thraupids are primitive, and nearly all the remainder are derived in this character. This is an example of the type of character conflicts that were discussed earlier, and because they are few, I think it probable that cluster 3 is correctly grouped by this synapomorphy. Thus cluster 3 is grouped by two independent characters (seed-eating adaptations and coracoidal head of the *deltoideus minor*).

Three lineages are shown arising from this branching point, though strict cladistic methodology demands only dichotomous branches. In order to resolve this it would be necessary to demonstrate some synapomorphy clustering two of the three branches, but I do not know of one.

The Cardinalinae resemble the Thraupidae in their colorful plumages and arboreal habits, but in their enlarged bills and habit of eating larger seeds (3a) appear to be more highly derived in feeding specializations than the emberizines. There is some variation in limb muscles (3b) but as only a few genera were dissected, the range of variation in the group is not well known.

The Emberizinae and Icteridae share a specialized ground foraging technique with both structural and behavioral aspects (3c). The other taxa in this assemblage are highly arboreal and seldom forage to any extent in open terrestrial habitats. They are also characterized in general by brightly colored, conspicuous plumages, at least in males. The emberizines in contrast are more terrestrial in foraging habits, and less brightly colored. Their plumages emphasize browns, grays, blacks, and sometimes yellows, and their backs are commonly streaked with brown and gray. Presumably this is associated with their ground foraging habits by making them less conspicuous to predators. The Icteridae appear

to have been derived from the emberizines through such forms as *Spiza*, *Dolichonyx*, and *Molothrus*, which resemble them in bill form and habits. Furthermore, many emberizines forage with a specialized type of movement, the bilateral scratch, in which they jump first forward and then backward with both legs simultaneously, scratching the substrate on the second jump to scatter surface litter and reveal food. At least two icterid genera, *Molothrus* and *Agelaius*, are known to use a similar foraging technique (Greenlaw, 1976).

The emberizines are very uniform in limb myology and most genera are inseparable on this basis. *Geospiza*, *Emberiza*, and *Loxia* lack the coracoid origin of *M. deltoideus minor*. This could be either a primitive state or a derived (secondarily primitive) condition. I have chosen the second alternative as shown in Fig. 10 (3i) because they so closely resemble the other emberizines in general, but the matter is uncertain. In view of the wide geographic separation between these genera, it is likely that this derived state arose independently in the three groups, so that cluster 3i may well be a false synapomorphy.

The Icteridae are clustered by two derived states, the loss of the patellar band and the Type 2 flexor digitorum profundus (3d). In most icterids the rectal bristles are either vestigial or completely lost (3e) as noted by Ridgway (1902:169). However, I have observed that the rectal bristles are well developed in *Spiza*, which myologically is allied with the Icteridae (3d). This supports the idea that *Spiza* is a primitive icterid, and a link to the emberizines.

The assumption of (3c), that ground-foraging is a synapomorphy of the Icteridae and Emberizinae, is contradicted by the arboreal habits of some icterids (3g) and the primitive Type 1 pronator profundus of a few (3h). If this suggestion is correct, then the apparently primitive states of cluster (3g) are presumably due to evolutionary reversal. The conflict is clearly unsettled, but I have chosen as most probable the scheme shown in Fig. 10 because (1) *Spiza* is so clearly an intermediate form between the two groups, and (2) the grossly enlarged bill of most genera in cluster (3g) is highly specialized and most certainly derived within this assemblage.

CLUSTER 4

This group includes the cardueline finches and the Drepanididae. The carduelines and the drepanidid genus *Psittirostra* are seedeaters that possess a more specialized biomechanical seed-cracking

system than that found in the emberizines and cardinalines. This was studied by Bock (1960), who termed it the "vise" method. It includes a stronger skull ossification, a restriction of the mobility of the upper jaw, and other features, and is thought to have evolved from the less specialized "nutcracker" system of the other members of cluster (3). It must be noted, however, that Bock's concept of "nutcracker" and "vise" systems of jaw biomechanics has been questioned (Zusi, 1961). The carduelines and drepanidids are also clustered by the reduction in size (leading in some cases to complete loss) of a hip muscle, *M. obturatorius lateralis dorsalis*.

Despite their diversity, the Carduelinae appear to be a coherent group on the basis of various structural and behavioral features (see Tordoff, 1954) as well as the presence of the vise method of seed cracking, and so the parsimonious suggestion that the group is monophyletic is a reasonable one. For this reason they are shown as having arisen from a single lineage (Fig. 10).

Several cardueline genera appear relatively primitive by the absence of a derived state, the tibial head of *M. peroneus brevis*. In terms of limb myology *Leucosticte* is the most primitive cardueline studied (4); the structure of the tongue also supports this view (Raikow, 1977b). Several other genera are more advanced in limb myology (4a, 4b).

CLUSTER 5

The development of the tibial head of *M. peroneus brevis*, a derived state, occurs in several other genera (cluster 5), which may be further clustered on other myological synapomorphies (5a, 5b, 5c). There is a character conflict in that the plantaris was apparently lost twice (at least) in the carduelines (4b, 5c), but the arrangement shown here is the most reasonable one given the distribution of the tibial head of the peroneus brevis.

CLUSTER 6

The derivation of the Drepanididae is treated in considerable detail elsewhere (Raikow, 1977b) and therefore will be considered here only briefly. It is difficult to demonstrate by strictly cladistic methods that the family Drepanididae is monophyletic; because of their incredible diversity, resulting from their adaptive radiation, they do not all share any clear-cut derived character states not also found among the Carduelinae. The argument for monophyly is based instead on the geographical restric-

tion to the Hawaiian Islands, the morphological intergradation between distinct adaptive types, and the remarkable uniformity of their limb muscles (Raikow, 1976, 1977a, 1977b).

Psittirostra is a finch-billed, seed-eating genus, whereas the other genera have bills adapted to a variety of feeding specializations. *Psittirostra* is

clearly the most primitive drepanidid genus, little modified from the cardueline ancestor that founded the family. A phylogeny of the genera of the Drepanididae is shown in Fig. 10 for the sake of completeness, but as I have analyzed it in detail elsewhere (Raikow, 1977b), I will not do so here.

PROPOSED CLASSIFICATION

Because of the diverse philosophies of classification now current, it is desirable to explain briefly the basis for a proposed classification. The school of phylogenetic systematics based on the ideas of Hennig includes both a methodology for reconstructing phylogenies, and a technique for constructing classifications based on those phylogenies. I accept the first but reject the second. Thus, although my phylogeny was derived by mostly Hennigian methods, my proposed classification is not.

In the Hennigian or cladistic method of classification the hierarchy of taxonomic categories is based directly on the branching pattern of the cladogram without regard to the nature or degree of evolutionary change (which may be quite variable) occurring between branching points. In a group of any size this will result in a large number of categories and of named taxa. The resulting classification is so complex and unwieldy as to be wholly impractical. Consider, for example, the classification of mammals proposed by McKenna (1975). This includes the categories (in alphabetical order) class, cohort, grandorder, infraorder, legion, magnorder, mirorder, order, parvorder, subclass, sublegion, supercohort, superlegion, and superorder. These are just the categories; the named taxa are much more numerous. The method does have the advantage that one can specify any monophyletic group in the cladogram by name. However, this can also be done more simply by referring to the group by the number of the branching point from which it arises. For instance, in referring to the group containing the Drepanididae plus those carduelines possessing the peroneus brevis tibial head (Fig. 10), one could specify, say, the "infrasupercohort Cardueloidida," but it is simpler (dare I say more parsimonious?) merely to say "cluster 5."

I also reject Hennigian classification because it is redundant, being merely verbal restatement of the cladogram. I prefer a classification in which evolutionary changes are considered, so that each tax-

on is characterized by some adaptive or other peculiarity that sets it apart from other taxa. If we are to have both phylogenies and classifications, why not let them serve different purposes? Critics claim that this results in subjectivity because different workers, given the same data, might produce different classifications. This may be true, but I see no fault in it. Different workers can emphasize the events that they consider to have been of the greatest biological significance in the history of the group. Mayr (1974) has effectively criticized cladistic classification, so I will not belabor the point further.

For most families I have not suggested subfamilies because I consider the basis for them to be uncertain or ambiguous. Future studies of intergeneric relationships may make subdivision of more families possible. My classification is not greatly different from those generally in use at the present time, as the limb myology has, in general, confirmed previous ideas of relationships. Several small families, such as the Cyclarhidae, Vireolaniidae, Tersinidae, and Catamblyrhynchidae, listed by Wetmore (1960), are not recognized because I have included their genera in other families of which they appear to be aberrant members. Inclusion of *Fringilla* with the cardueline finches unfortunately necessitates the use of the name Fringillinae for the combined group, although I would have preferred to retain the name Carduelinae.

Each family recognized appears to be a coherent group. The Vireonidae includes *Cyclarhis* and *Vireolanius* because of their anatomical similarity, as pointed out by several other authors. The Parulidae are essentially arboreal insectivores, with occasional lines specializing in different directions, as with *Seiurus* and the nectar-feeders. The Thraupidae are essentially arboreal fruit and insect eaters. This family is still the least understood, and may by polyphyletic, but recognition of a single family is the most practical course on the basis of our present

understanding. The Fringillidae are seed-eaters. The Cardinalinae are basically heavy-billed types using the nutcracker method of seed breaking, and with colorful plumages. The Emberizinae are essentially smaller-billed nutcracker types, with emphasis on ground foraging. The Fringillinae (Carduelinae) are mainly short-legged, arboreal seedeaters with a heavy bill, using the vise method of seed cracking. The Icteridae, despite their considerable diversity, are marked by a specialized bill-gaping feeding mechanism. The line between Fringillinae and Drepanididae is vague and admittedly arbitrary. However, I feel that the Hawaiian Honeycreepers merit family rank because they are unquestionably the product of a single adaptive radiation in a geographic region where no other members of the assemblage occur naturally.

The sequence of families given here is, in my opinion, the most reasonable solution to the prob-

lem of expressing a multidimensional branching pattern in a linear order. In any linear sequence of the families of oscines, the sequence from the Parulidae onward should be kept intact, with no other families interposed. This follows from the monophyly of the group. The position of the Vireonidae, however, remains problematical because their affinities are still obscure.

Proposed Classification:

Vireonidae

Parulidae

Thraupidae

Fringillidae

 Cardinalinae

 Emberizinae

 Fringillinae

Drepanididae

Icteridae

CONCLUSIONS

1. The hypothesis that the New World nine-primaried oscines form a monophyletic group is supported by the comparative anatomy of the limb muscles for all groups except the Vireonidae. For all other groups the muscles show a common general pattern with a series of gradual evolutionary changes consistent with a scheme of adaptive radiation presented in a phylogenetic hypothesis.
2. The Vireonidae do not share derived character states with the other groups and cannot be included with them in a single phylogeny. The shrike-vireos and peppershrikes share unique derived states with the vireos, and it is recommended that all be included in a single family whose monophyletic nature is indicated by their synapomorphies.
3. The limb myology indicates that the Parulidae are a primitive but fairly cohesive group which is probably monophyletic. This conclusion is based more on the general similarity of most genera than on the existence of any clear-cut synapomorphies. The "coerebid" genera *Coereba* and *Conirostrum* are included. *Peucedramus* does not fit into this family but probably belongs with the Sylviidae. *Icteria* and *Seiurus* are aberrant in limb muscles but the significance of this is uncertain. *Zeledonia* is myologically primitive, and may reasonably be included in the Parulidae near *Basileuterus*.
4. The Thraupidae are myologically heterogeneous and may be polyphyletic. *Nephelornis* and *Urothraupis* are very similar and relatively primitive. Their exact position is uncertain but is at the parulid/thraupid border. It is somewhat arbitrarily suggested that they be placed in the Thraupidae. The "coerebid" tanagers fit easily within the Thraupidae, but the question of their monophyly as nectar feeders is unsettled. *Rhodinocichla*, *Tersina*, and *Catamblyrhynchus* are best treated as aberrant thraupids whose intergeneric affinities are obscure.
5. The Emberizinae and Icteridae may be sister-groups on the basis of terrestrial foraging habits and techniques. The limb myology is consistent with the hypotheses that both are monophyletic groups. *Spiza* is a primitive icterid close to the Emberizinae. The orioles, caciques, and oropendolas are secondarily arboreal.
 - i. The Cardinalinae are somewhat diverse in limb myology and their phylogenetic position is probably close to the emberizine/icterid group.
7. The Carduelinae are diverse in limb myology, with *Leucosticte* and *Fringilla* being relatively primitive within the group. The hypothesis of monophyly is supported by a derived jaw mech-

anism and a pattern of derived limb muscle features.

8. The Drepanididae are almost certainly monophyletic as indicated by geographical distribution and morphological intergradation. They arose from a single cardueline founder species.
9. Based on the foregoing phylogenetic study, the general taxonomic recommendation arising from this investigation follows from a belief that the family category should be used for grouping rather than separating forms, and that families with one or a very few genera should be avoided as much as possible. For the most part I will not

suggest subfamily groups because I consider the basis for most to be uncertain or ambiguous.

Proposed Classification:

Vireonidae
 Parulidae
 Thraupidae
 Fringillidae
 Cardinalinae
 Emberizinae
 Fringillinae
 Drepanididae
 Icteridae

ACKNOWLEDGMENTS

Extensive anatomical studies would not be possible without the generous cooperation of individuals and institutions in providing loans of specimens for dissection. Materials used in the present study were provided by A. J. Berger (University of Hawaii); P. J. K. Burton (British Museum, Natural History, Tring); Mary H. Clench (Carnegie Museum of Natural History, Pittsburgh); Ned K. Johnson (Museum of Vertebrate Zoology, University of California, Berkeley), George H. Lowery, Jr., and John P. O'Neill (Louisiana State University Museum of Zoolo-

gy, Baton Rouge); Charles G. Sibley (Peabody Museum of Natural History, Yale University, New Haven); and Richard L. Zusi (National Museum of Natural History, Washington, D.C.). The services of the Museum of Vertebrate Zoology are supported by NSF Grant BMS 7200102. I am grateful to Kenneth C. Parkes, Harrison B. Tordoff, and Richard L. Zusi for reading and criticizing the manuscript, and to Mary H. Clench for many helpful suggestions. Supported by NSF grants DEB76 20337 and BMS74 18079.

LITERATURE CITED

- AMES, P. L. 1975. The application of syringeal morphology to the classification of the Old World insect eaters (Muscicapidae). *Bonn. Zool. Beitr.*, 26:107-134.
- BEECHER, W. J. 1951a. Convergence in the Coerebidae. *Wilson Bull.*, 63:274-287.
- . 1951b. Adaptations for food-getting in the American blackbirds. *Auk*, 68:411-440.
- . 1953. A phylogeny of the oscines. *Auk*, 70:270-333.
- BENTZ, G. D. 1976. The appendicular myology and phylogenetic relationships of the Ploceidae and Estrildidae (Aves: Passeriformes). Unpublished Ph.D. dissert. Univ. Pittsburgh, Pittsburgh, Pennsylvania, 157 pp.
- BERGER, A. J. 1966. The musculature. Pp. 224-473, *Avian myology* (J. C. George and A. J. Berger, eds.) Academic Press, New York and London, 500 pp.
- . 1968. Appendicular myology of Kirtland's Warbler. *Auk*, 85:594-616.
- . 1969. Appendicular myology of passerine birds. *Wilson Bull.*, 81:220-223.
- BLAKE, E. R. 1968. Family Vireonidae, peppershrikes, shrike-vireos, and vireos. Pp. 103-138, *in* Check-list of birds of the world (R. A. Paynter, Jr., ed.), *Mus. Comp. Zool.*, Cambridge, Massachusetts, 14:1-433.
- BOCK, W. J. 1960. The palatine process of the premaxilla in the Passeres. *Bull. Mus. Comp. Zool.*, 122:361-488.
- . 1962. The pneumatic fossa of the humerus in the Passeres. *Auk*, 79:425-443.
- . 1965. The role of adaptive mechanisms in the origin of higher levels of organization. *Syst. Zool.*, 14:272-287.
- BOCK, W. J., and R. Shear. 1972. A staining method for gross dissection of vertebrate muscle. *Anat. Anz.*, 130:222-227.
- CLARK, G. A., Jr. 1974. Foot-scuttle differences among certain North American oscines. *Wilson Bull.*, 86:104-109.
- CLENCH, M. H., and O. L. Austin, Jr. 1974. *Passeriformes*. *Encyclopedia Britannica*, Inc., 5th ed., pp. 1052-1066.
- DELACOUR, J. 1972. Hybrids Sugar-bird × tanager (*Cyanerpes cyaneus* × *Tangara nigrocincta franciscae*). *Avicult. Mag.*, 78:187-188.
- EISENMANN, E. 1962a. On the genus "*Chamaethlypis*" and its supposed relationship to *Icteria*. *Auk*, 79:265-267.
- . 1962b. On the systematic position of *Rhodinocichla rosea*. *Auk*, 79:640-648.
- FICKEN, M. S., and R. W. Ficken. 1962. Some aberrant characters of the Yellow-breasted Chat, *Icteria virens*. *Auk*, 79:718-719.
- GAUNT, A. S. 1969. Myology of the leg in swallows. *Auk*, 86:41-53.
- GEORGE, J. C., and A. J. BERGER. 1966. *Avian myology*. Academic Press, New York and London, 500 pp.
- GEORGE, W. G. 1962. The classification of the Olive Warbler, *Peucedramus taeniatus*. *Amer. Mus. Novit.*, 2103:1-41.
- . 1968. A second report on the basihyale in American songbirds, with remarks on the status of *Peucedramus*. *Condor*, 70:392-393.

- GREENLAW, J. S. 1976. Use of bilateral scratching behavior by emberizines and icterids. *Condor*, 78:94-97.
- HUNT, J. H. 1971. A field study of Wrenthrush, *Zeledonia coronata*. *Auk*, 88:1-20.
- KLUGE, A. G. 1977. Concepts and principles of morphologic and functional studies. Pp. 1-27, in *Chordate structure and function* (A. G. Kluge, ed.), Macmillan Publ. Co., New York, 2nd ed., 628 pp.
- LOWERY, G. H., Jr., and B. L. Monroe, Jr. 1968. Family Parulidae, Wood Warblers. Pp. 3-93, in *Check-list of birds of the World* (R. A. Paynter, Jr., ed.), *Mus. Comp. Zool.*, Cambridge, Massachusetts, 14:1-433.
- LOWERY, G. H., Jr., and D. A. TALLMAN. 1976. A new genus and species of nine-primaried oscine of uncertain affinities from Peru. *Auk*, 93:415-428.
- LOWTHER, P. A. 1975. Geographic and ecological variation in the family Icteridae. *Wilson Bull.*, 87:481-495.
- MAYR, E. 1955. Comments on some recent studies of song bird phylogeny. *Wilson Bull.*, 67:33-44.
- . 1974. Cladistic analysis or cladistic classification? *Zool. Syst. Evol.-forsch.*, 12:94-128.
- . 1976. The emergence of evolutionary novelties. Pp. 88-113, in *Evolution and diversity of life* (E. Mayr, ed.), Harvard Univ. Press, Cambridge, Massachusetts, 721 pp.
- MAYR, E., and D. Amadon. 1951. A classification of recent birds. *Amer. Mus. Novit.*, 1496:1-42.
- McKENNA, M. C. 1975. Toward a phylogenetic classification of the Mammalia. Pp. 21-46, in *Phylogeny of the Primates* (W. P. Luckett and F. S. Szalay, eds.), Plenum Publ. Corp., New York, 483 pp.
- PAYNTER, R. A., Jr. 1970. Subfamily Catamblyrhynchinae. P. 215, in *Check-list of birds of the World* (R. A. Paynter, ed.), *Mus. Comp. Zool.*, Cambridge, Massachusetts, 13:1-443.
- . 1970. Subfamily Emberizinae, Buntings and American Sparrows. Pp. 3-214, in *Check-list of birds of the World* (R. A. Paynter, ed.), *Mus. Comp. Zool.*, Cambridge, Massachusetts, 13:1-443.
- RAIKOW, R. J. 1975. The evolutionary reappearance of ancestral muscles as developmental anomalies in two species of birds. *Condor*, 77:514-517.
- . 1976. Pelvic appendage myology of the Hawaiian Honeycreepers (Drepanididae). *Auk*, 93:774-792.
- . 1977a. Pectoral appendage myology of the Hawaiian Honeycreepers (Drepanididae). *Auk*, 94:331-342.
- . 1977b. The origin and evolution of the Hawaiian Honeycreepers (Drepanididae). *The Living Bird*, 15:95-117.
- ROSS, H. H. 1974. *Biological systematics*. Addison-Wesley, Reading, Massachusetts, 345 pp.
- RIDGWAY, R. 1902. The birds of North and Middle America, Part II. *Bull. U.S. Nat. Mus.* 50:1-834.
- SCHAEFER, C. W. 1976. The reality of the higher taxonomic categories. *Z. Zool. Syst. Evolut.-forsch.*, 14:1-10.
- SHORT, L. L., Jr., and C. S. Robbins. 1967. An intergeneric hybrid Wood Warbler (*Seiurus* × *Dendroica*). *Auk*, 84:534-543.
- SIBLEY, C. G. 1968. The relationships of the "wren-thrush," *Zeledonia coronata* Ridgway. *Postilla*, 125:1-12.
- . 1970. A comparative study of the egg-white proteins of passerine birds. *Bull. Peabody Mus. Nat. Hist.*, Yale Univ., 32:1-131.
- SKUTCH, A. F. 1962. On the habits of the Queo, *Rhodinocichla rosea*. *Auk*, 79:633-639.
- STALLCUP, W. B. 1954. Myology and serology of the avian family Fringillidae, a taxonomic study. *Univ. Kansas Publ., Mus. Nat. Hist.*, 8:157-211.
- STORER, R. W. 1969. What is a tanager? *The Living Bird*, 8:127-136.
- SUSHKIN, P. P. 1925. The Evening Grosbeak (*Hesperiphona*), the only American genus of a Palearctic group. *Auk*, 42:256-261.
- . 1929. On the systematic position of the Drepanididae. *Proc. Internat. Ornith. Congr.*, 6:379-381.
- TORDOFF, H. B. 1954. A systematic study of the avian family Fringillidae based on the structure of the skull. *Mus. Zool. Misc. Publ.*, Univ. Michigan, 81:1-42.
- VAN TYNE, J., and A. J. Berger. 1976. *Fundamentals of ornithology*. John Wiley & Sons, New York, 2nd ed., 808 pp.
- WETMORE, A. 1960. A classification for the birds of the world. *Smithsonian Misc. Coll.*, 139(11):1-37.
- ZUSI, R. 1961. [Review of] Bock, W. J., 1960, The palatine process of the premaxilla in the passerines, *Bull. Mus. Comp. Zool.*, 122:361-488. *Auk*, 78:101-102.